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## The Genus *Trichocolea* in North, Central, and South America—(Hepaticae)\*

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### INTRODUCTION AND HISTORY

The genus *Trichocolea* was first proposed by Dumortier (1822), as *Thricholea*, for the species *Jungermannia tomentella* Ehrhart, thus separating this species from the old genus *Jungermannia*. In 1829, Dumortier altered the original spelling to *Tricholea* and following this, in 1831, he recorded the name as *Thricolea* on pages 24, 25, and 66 and as *Tricolea* in the table of contents of the same paper. Subsequently, in 1835, he returned to the spelling *Tricholea*. Later, Nees (1838) corrected the spelling to *Trichocolea* and this spelling has been widely accepted. Lindberg (1875) proposed the genus *Leiomitra* for the tropical species *Jungermannia tomentosa* described by Swartz and two years later, Trevisan (1877) proposed the genus *Basichilon* for the same species.

Various later authors have used one or another of these names. However, the name *Trichocolea* has been adopted as a *nomen genericum conservandum* by action of the VIII International Botanical Congress, 1954.

Gottsche (1864) subdivided the genus *Trichocolea* into two sections—Section *Hirtiflora* in which the calyptra is fused with, and surrounded by, the bracts and bracteoles as represented by the species *Trichocolea tomentella*, *T. mollissima* (New Zealand), and *T. lanata* (New Zealand); and Section *Laeviflora* in which the calyptra is smooth and free as in

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*Gymnomitrium*. This latter section was represented by *Trichocolea tomentosa*. *T. tomentella* was the type for the Section *Hirtiflora* and *T. tomentosa* was the type for the Section *Laeviflora*. Lindberg, however, considered Gottsche's Section *Laeviflora* as deserving of generic status and it was upon this basis that he proposed his generic name *Leiomitra*. Two years later, Trevisan proposed the name *Basichiton* for this same section.

Spruce (1885) adopted the generic name *Leiomitra* for his South American species, but stated in his discussion of the genus that there was little to differentiate *Leiomitra* from *Trichocolea*. Later (Spruce, 1893), he used the name *Trichocolea* and reduced *Leiomitra* to sub-generic rank. Both Stephani (1909-12) and Knapp (1930) have shown that the differences in sporophyte development between *T. tomentella* and *T. tomentosa* are so slight as to merit no generic distinction.

Until quite recently, the genus *Trichocolea* was considered a member of the Ptilidiaceae, but in 1954, K. Müller (1954, p. 586) proposed the new family Trichocoleaceae for it. When one considers the marked differences between *Trichocolea* and the other genera in the Ptilidiaceae, this separation seems to be justified. A perianth is present in the rest of the Ptilidiaceae while in *Trichocolea*, a club-shaped or globose, thick-walled prolongation of the stem tissue encloses the sporophyte.

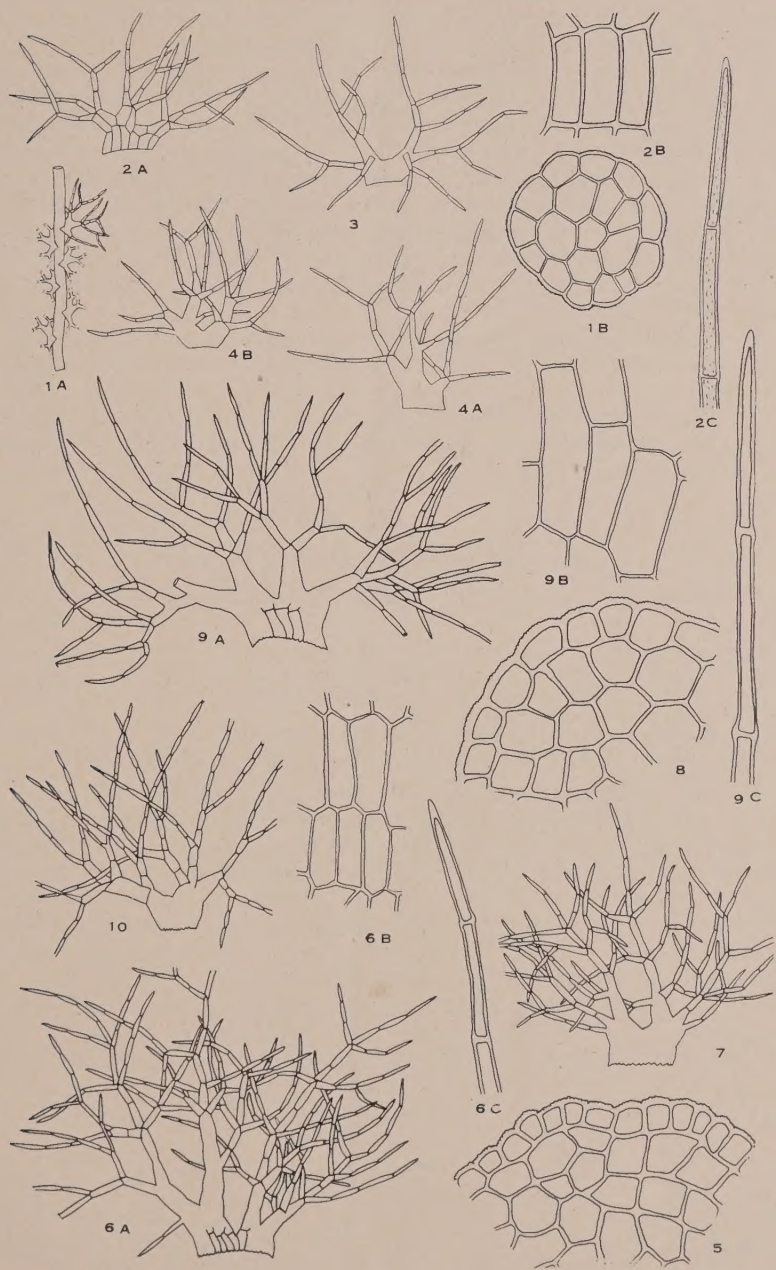
Of the 48 species recognized under this genus by Stephani in his *Species Hepaticarum* (1909-12; 1924), 29 species, including *T. Biddlecomiae* which he placed in synonymy under *T. tomentella*, were reported from the Americas. One species, *T. elegans* was erroneously listed among the Australian species. Since the completion of Stephani's Monograph, three additional species have been described. Of the 33 species studied, 20 are here reduced to synonymy. One variety is not included because the original collection was not available for study.

The writer wishes to express his appreciation to the persons and institutions who have assisted in the preparation of this monograph. The location of the individual specimens has been designated by the symbols enumerated as follows: (F) the private herbarium of Dr. Margaret Fulford; (G) Conservatoire et Jardin Botaniques, Geneva (material from the Stephani Collection); (FH) the Farlow Library and

#### EXPLANATION OF FIGURES 1-10

FIGS. 1-4. *Trichocolea filicaulis* Steph. 1A. Portion of a stem showing leaf insertion, dorsal view,  $\times 12$ . 1B. Cross-section of a stem,  $\times 235$ . 2A. Stem leaf,  $\times 55$ . 2B. Cells from the lamina of a leaf,  $\times 235$ . 2C. Portion of a cilium,  $\times 235$ . 3. Stem underleaf,  $\times 55$ . 4A. Stem leaf,  $\times 55$ . 4B. Stem underleaf,  $\times 55$ . FIGS. 5-7. *Trichocolea floccosa* Herzog & R. Hatcher. 5. Portion of a stem cross-section,  $\times 235$ . 6A. Stem leaf,  $\times 55$ . 6B. Cells from the lamina of a leaf,  $\times 235$ . 6C. Portion of a cilium,  $\times 235$ . 7. Stem underleaf,  $\times 55$ . FIGS. 8-10. *Trichocolea Sprucei* Steph. 8. Portion of a stem cross-section,  $\times 235$ . 9A. Stem leaf,  $\times 55$ . 9B. Cells from the lamina of a leaf,  $\times 235$ . 9C. Portion of a cilium,  $\times 235$ . 10. Stem underleaf,  $\times 55$ . FIGS. 1-3, drawn from a portion of the original material from Guadeloupe (G). FIGS. 4A and 4B, from a portion of the original material of *T. paupercula* Steph. from Bolivia (G). FIGS. 5-7, from a portion of the original material from Costa Rica (Hb. Herzog). FIGS. 8-10, from a portion of the original material from Dominica (Manch.).





Herbarium of Cryptogamic Botany, Harvard University, Cambridge, Mass. (including material from the Stephani Herbarium); (Manch.) Univ. of Manchester (material from the Spruce Collection); (NY) herbarium of the New York Botanical Garden (including material from the Mitten and Spruce Collections); (S-PA) Paleobotanical Department, Swedish Museum of Natural History, Stockholm (with special thanks to Dr. Herman Persson for making available a portion of the original material of *Jungermannia tomentosa* Swartz); (Hb. Herzog) the private herbarium of Dr. Theodor Herzog of Jena (with special thanks to Dr. Herzog for the loan of a portion of the types of *T. argentea*, *T. pterophylla*, and *T. floccosa*); (SM) the Sullivant Moss Herbarium, Hepaticae, of the American Bryological Society, at the University of Cincinnati.

I also wish to acknowledge the generous assistance of the staff of the Lloyd Library of Cincinnati for their aid in locating many valuable references.

To Dr. Margaret Fulford of the University of Cincinnati, for her invaluable suggestions and criticisms and for reading the manuscript, the writer is deeply grateful.

#### CHARACTERS OF THE GENUS TRICHOCOLEA

TRICHOCOLEA Dumort., corr. Nees, *Naturg. Eur. Leberm.* **3**: 103. 1838.

*Tricholea* Dumort., *Comm. Bot.* 113. 1822.

*Tricholea* Dumort., *Anal. Fam.* 69. 1829. nomen nudum.

*Tricholea* Dumort., *Sylog. Jungerm.* 24, 28, 66. 1831.

*Tricholea* Dumort., op. cit. p. 99.

*Leiomitra* Lindb., *Soc. Sci. Fenn. Acta* **10**: 515. 1875.

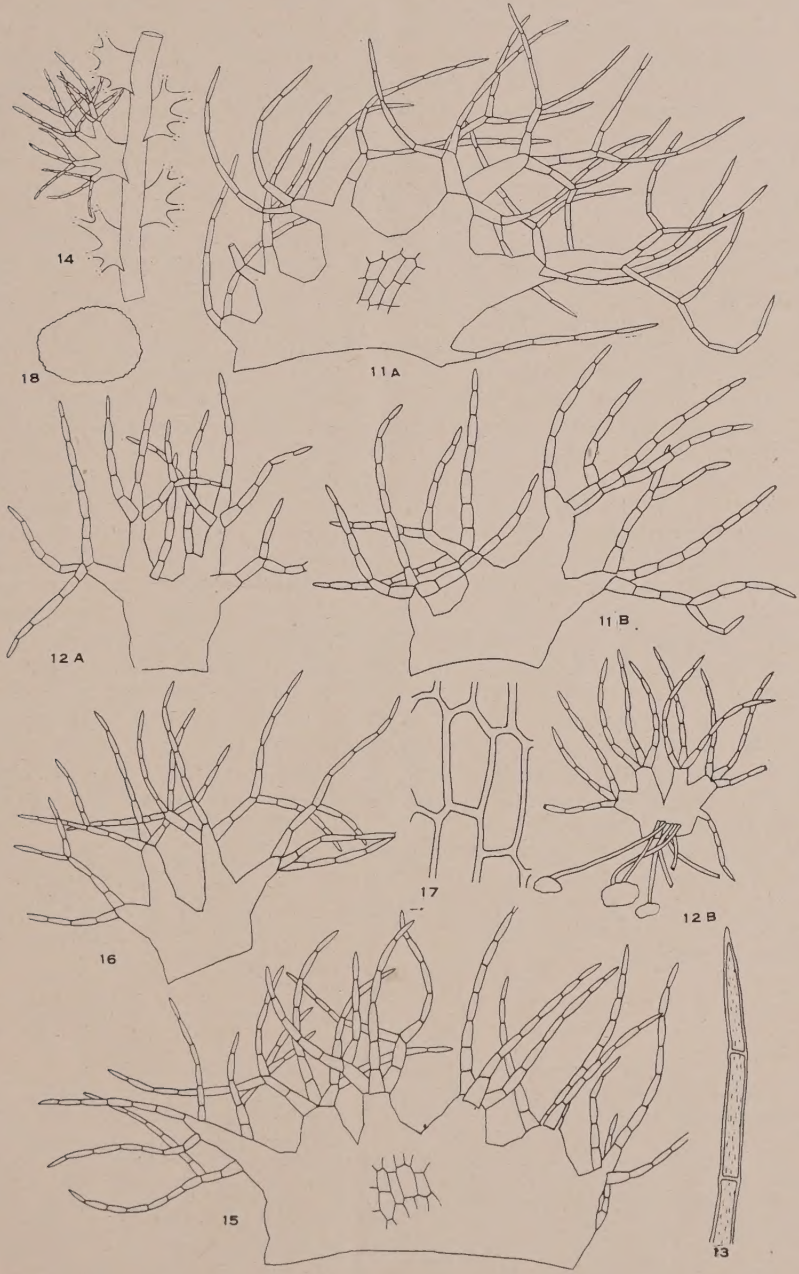
*Basichiton* Trev., *R. Ist. Lombardo Mem. Sci. Math. Nat.* **13**: 394. 1877.

Plants in tufts, mats, or scattered among other bryophytes, prostrate to suberect, whitish-green to yellowish-green; stems filiform to robust, simple to tripinnately branched, the vegetative branches of the *Frullania* type (from the ventral half of a lateral segment) and forming an angle of about 90 degrees, or as subflora innovations below the female inflorescence; cells of the stem little differentiated, mostly thin-walled, the cortical cells of varying number, in one to several layers, usually shorter and with a smaller diameter than the cells of the medulla, the cuticle thickened, striolate-papillose; subfloral innovations 1-3, similar to the stem, of unlimited growth, often terminated by a sporophyte with subfloral innovations: rhizoids when present colorless, in clusters

#### EXPLANATION OF FIGURES 11-18

FIGS. 11-18. *Trichocolea flaccida* (Spruce) Jack & Stephani. 11A. Stem leaf,  $\times 55$ . 11B. Branch leaf,  $\times 55$ . 12A. Stem underleaf,  $\times 55$ . 12B. Branch underleaf,  $\times 55$ . 13. Portion of a cilium,  $\times 235$ . 14. Portion of a stem showing leaf insertion, dorsal view,  $\times 25$ . 15. Male bract,  $\times 55$ . 16. Male bracteole,  $\times 55$ . 17. Cells from the lamina of a leaf,  $\times 235$ . 18. Cross-section of a stem,  $\times 55$ . FIGS. 11-18, drawn from a portion of *T. (Leiomitra) flaccida* Spruce, *Hepat. Spruc.*, from Mt. Campana, Peru (NY).



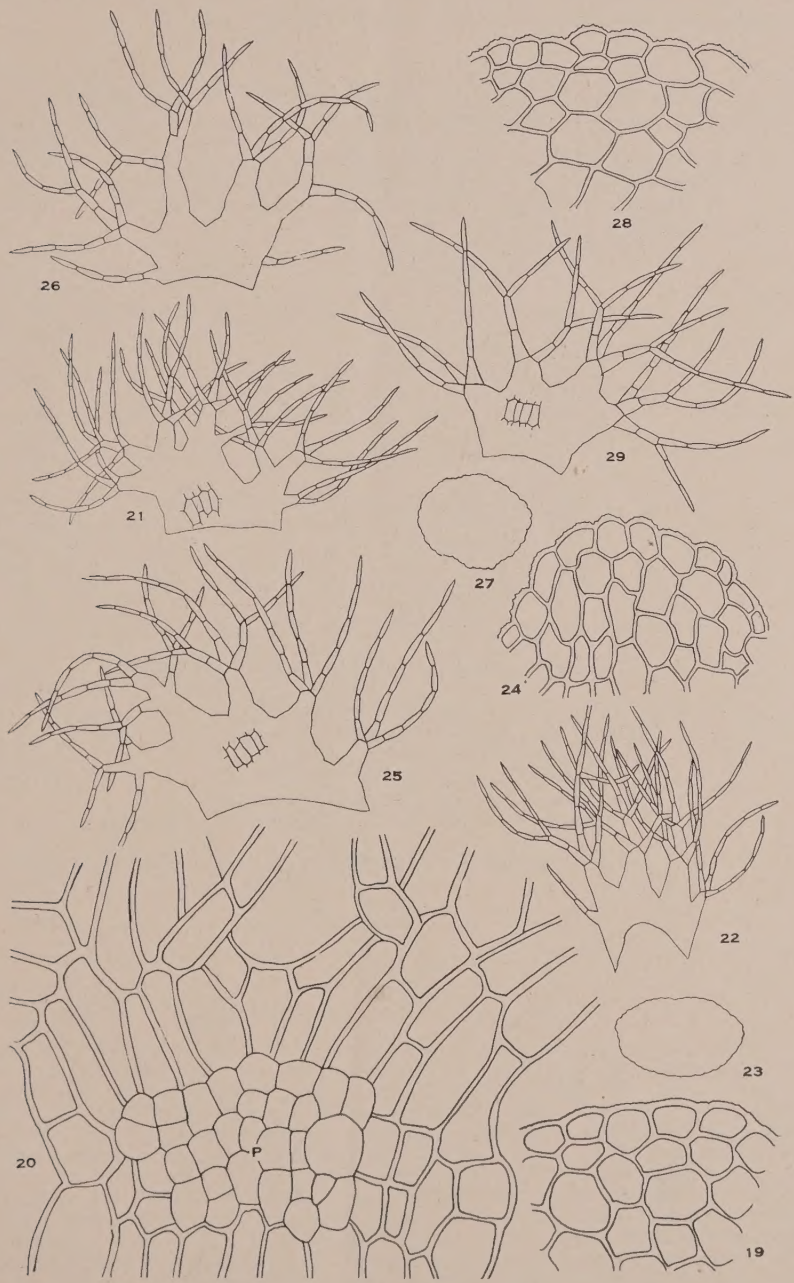


from a unistratose, disc-shaped pad on the lamina of the underleaf, rarely from a male bracteole, separate, or fused and ending in entire or deeply lobed plates; paraphyllia sometimes present on stems and branches, green, to 8 cells long, often branched; leaves succubous, alternate, attached in an oblique line, distant to imbricated, spreading, sometimes decurved, ovate to reniform in outline, asymmetrical with the ventral portion the larger, or subsymmetrical, deeply divided into 3-9 unequal, simple or divided segments; the segment triangular in outline, sparsely to densely ciliate with whorled or opposite, usually long, simple or branched cilia; the lamina 1-18 cells long, cells rectangular to quadrate or hexagonal in outline; the cuticle striolate-papillose; underleaves smaller, distant to imbricated, symmetrical, attached in a transverse line, sometimes connate with the leaves on one side of the stem, deeply bifid and divided to one half or nearly to the base into usually four segments, ciliate as in the leaves; the cells similar to those of the leaves: dioicous; male branches similar to the vegetative branches, the bracts in 15 or more series, concave, similar to the leaves but with a longer lamina and shorter segments, ciliate; antheridia large, globose, solitary or in pairs in the axils of bracts; bracteoles similar to the underleaves: female inflorescence terminal on a main stem or branch, becoming axillary or lateral by development of subfloral innovations; bracts and bracteoles in three series, closely imbricated, the innermost series the largest; bracts symmetrical to asymmetrical, larger than the leaves and deeply divided into usually more segments, ciliate as in the leaves; bracteoles similar to the underleaves but larger: archegonia in groups of 8-20 or more, surrounded by a dense development of paraphyllia: true perianth absent: the sporophyte enclosed in a club-shaped or globose, thick-walled prolongation of the stem tissue (coelocaulis or stem perianth), usually covered with paraphyllia and bearing numerous archegonia in the upper part: the sporangium oblong, borne on a long, thick stalk and dehiscing by four valves, the capsule wall (in *T. tomentella*) of 6-7 cell layers, the outermost layer of large thin-walled cells, the inner layers of smaller cells with rod-shaped, reddish-brown thickenings on the tangential walls; the sporangium stalk long and thick; elaters long, slender, reddish-brown, with 2-3 spirals, the ends rounded or tapering; spores 30-35  $\mu$  (in *T. paraphyllina*), reddish-brown, oval to rounded, smooth or minutely punctate.

#### EXPLANATION OF FIGURES 19-29

FIGS. 19-29. *Trichocolea flaccida* (Spruce) Jack & Stephani. 19. Portion of a stem cross-section,  $\times 235$ . 20. Portion of a stem underleaf showing rhizoid pad (P),  $\times 235$ . 21. Stem leaf,  $\times 55$ . 22. Stem underleaf,  $\times 55$ . 23. Cross-section of a stem,  $\times 55$ . 24. Portion of a stem cross-section,  $\times 235$ . 25. Stem leaf,  $\times 55$ . 26. Stem underleaf,  $\times 55$ . 27. Cross-section of a stem,  $\times 55$ . 28. Portion of a stem cross-section,  $\times 235$ . 29. Stem leaf,  $\times 55$ . FIGS. 19-20, drawn from a portion of *T. (Leiomitra) flaccida* Spruce, *Hepat. Spruc.*, from Mt. Campana, Peru (NY). FIGS. 21-24, from a portion of the original material of *T. Herzogii* Steph., from Bolivia. FIGS. 25-28, from a portion of the original material of *T. patula* Steph. from Dominica (G). FIG. 29, from a portion of the material of *T. tomentosa* var. *canelensis* Spruce, *Hepat. Spruc.*, from Ecuador (NY).





Type: *Trichocolea tomentella* (Ehrh.) Dumort. ex Nees, 105. 1838.  
[*Jungermannia tomentella* Ehrh., Beitr. Naturk. 2: 150. 1788.]

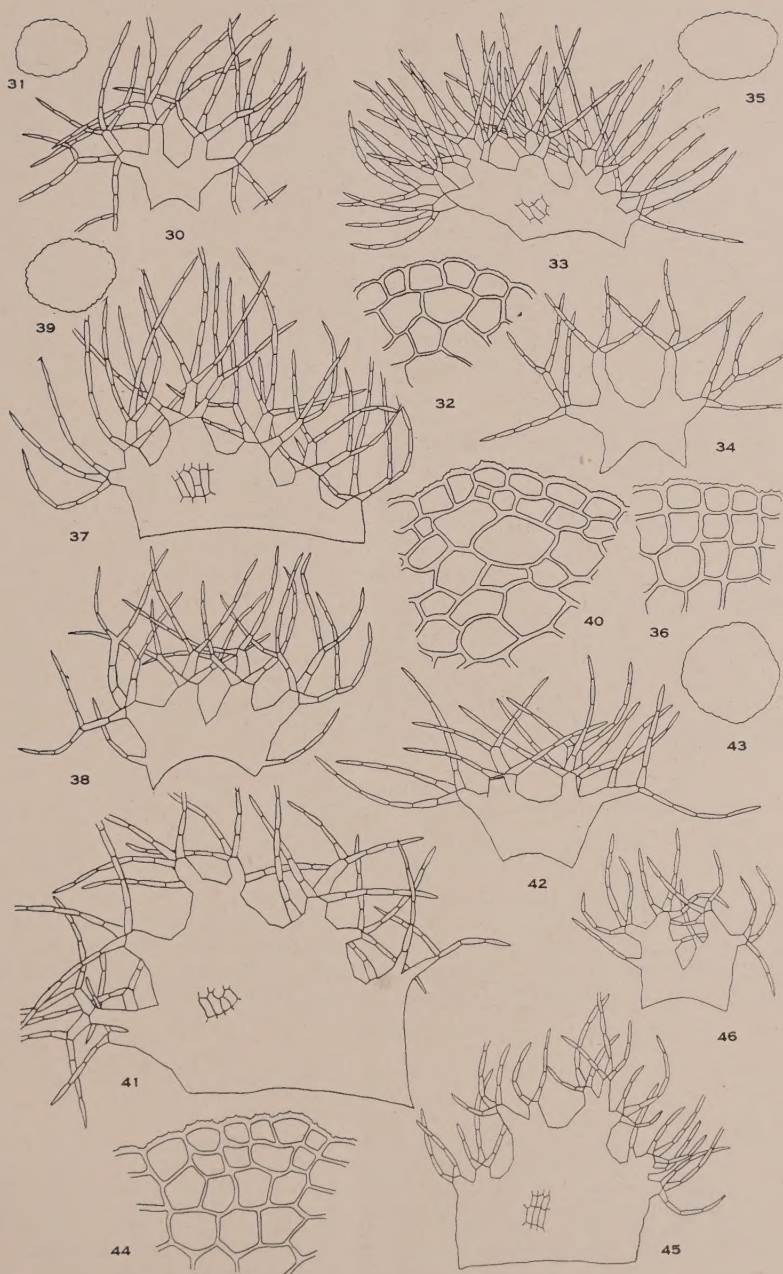
#### KEY TO THE AMERICAN SPECIES OF TRICHOCOLEA

- a. Leaves divided into only three segments; plants very small, filiform.....1. *T. filicaulis*
- a. Leaves divided into more than three segments; plants larger.....b.
- b. Lamina of the leaf at least half as long as broad, usually 5 or more cells long. c.
- c. Lamina of the leaf bearing scattered superficial cilia.....10. *T. argentea*
- c. Lamina without superficial cilia.....d.
- d. Stems bearing paraphyllia.....e.
- e. Leaves divided to one half into 4-6 sparsely ciliate segments.....7. *T. paraphyllina*
- e. Leaves divided to one half into 6-8 very densely ciliate segments.....9. *T. robusta*
- d. Stems without paraphyllia.....f.
- f. Leaf segments with the cilia recurved.....8. *T. elegans*
- f. Leaf segments with cilia not recurved.....g.
- g. Lamina of the leaves 8-14 cells long, not distinctly broader than long.....5. *T. brevifissa*
- g. Lamina of the leaf 5-6 cells long, distinctly broader than long.....h.
- h. Plants small to medium; leaves divided to two thirds into 4-5 mostly sparsely ciliate segments; leaves not decurrent.....4. *T. flaccida*
- h. Plants medium to large; leaves divided to one half into 5-6 densely ciliate segments; leaves often somewhat decurrent dorsally.....6. *T. Elliottii*
- b. Lamina of the leaf less than half as long as broad, usually only 1-3 cells long.....i.
- i. Plants regularly bi-tripinnate; stems bearing paraphyllia.....13. *T. tomentella*
- i. Plants pinnate to irregularly bipinnate; stems without paraphyllia.....j.
- j. Plants large, leaves imbricated, appressed to the stem.....k.
- k. Leaves with a very long dorsal insertion.....11. *T. Uleana*
- k. Leaves with a short dorsal insertion.....12. *T. tomentosa*
- j. Plants small, leaves approximate, spreading.....1.
- 1. Lamina of the leaf one cell long, the cells averaging  $55 \times 18 \mu$ .....2. *T. floccosa*
- 1. Lamina of the leaf 1-2 cells long, the cells averaging  $91 \times 29 \mu$ .....3. *T. Sprucei*

#### EXPLANATION OF FIGURES 30-46

FIGS. 30-40. *Trichocolea flaccida* (Spruce) Jack & Stephani. 30. Stem underleaf,  $\times 55$ . 31. Cross-section of a stem,  $\times 55$ . 32. Portion of a stem cross-section,  $\times 235$ . 33. Stem leaf,  $\times 55$ . 34. Stem underleaf,  $\times 55$ . 35. Cross-section of a stem,  $\times 55$ . 36. Portion of a stem cross-section,  $\times 235$ . 37. Stem leaf,  $\times 55$ . 38. Stem underleaf,  $\times 55$ . 39. Cross-section of a stem,  $\times 55$ . 40. Portion of a stem cross-section,  $\times 235$ . FIGS. 41-46. *Trichocolea brevifissa* Steph. 41. Stem leaf,  $\times 55$ . 42. Stem underleaf,  $\times 55$ . 43. Cross-section of a stem,  $\times 55$ . 44. Portion of a stem cross-section,  $\times 235$ . 45. Stem leaf,  $\times 55$ . 46. Stem underleaf,  $\times 55$ . FIGS. 30-32, drawn from a portion of *T. tomentosa* var. *canelensis* Spruce, Hepat. Spruc., from Ecuador (NY); 33-36 from a portion of the original material of *T. Eggersiana* Steph. from Dominica (G); 37-40 from a portion of *T. inaequalis* Steph. from Guatemala (G); 41-44 from a portion of the original material of *T. cubensis* Steph. from Cuba (G); 45-46 from a portion of *T. subquadrata* Steph. from Trinidad, collected by Crüger (G; FH).





1. *TRICHOCOLEA FILICAULIS* Steph., Spec. Hepat. 4: 59. 1909.

*T. paupercula* Steph., Bibliotheca Bot. 87: 230. 1916.

Plants in tufts, pale, yellowish-green: stems with leaves to 1 mm. wide, 2–3 cm. long, simple to irregularly pinnate, stem in cross-section, oval to orbicular, to 5 cells in diameter; cells of the medulla averaging 28  $\mu$ , cells of the cortex in a single layer, averaging 22  $\mu$ , cuticle thickened, striolate-papillose; paraphyllia absent; branches mostly 2–3 cm. long; rhizoids not seen: leaves distant to approximate, spreading, asymmetrical, to 0.5 mm. long, 0.8 mm. wide, divided to three fourths into three unequal segments; the segment triangular in outline, with a few long, simple or branched cilia; the lamina 1–2 cells long, cells rectangular in outline, averaging 63  $\mu$  long, 22  $\mu$  wide; the cuticle striolate-papillose: underleaves usually as large as the leaves, deeply bifid, cilia similar to those of the leaf; branch leaves and underleaves similar to those of the stem: male and female inflorescence and sporophyte not seen. (Figs. 1–4A, B).

Habitat: On bark.

The distinguishing characteristics of this species include its very small size and its leaves with only three sparsely ciliate segments.

Distribution: Guadeloupe: without locality, L'Herminier, the original collection, (G).—Dominican Republic: Santo Domingo, without locality, Elliott, (G).—Bolivia: Comorapa, Herzog, no. 4314, the original material of *T. paupercula*, (G); Sillar, Herzog, no. 2697: San Mateo-Sunchal, Herzog, no. 4492, cited by Herzog (1916, 230).

In 1916, Stephani described *T. paupercula* from Bolivia, but a study of the original material indicates that it is indistinguishable from *T. filicaulis*. The growth habit and leaves of the two are identical. While the underleaves of *T. paupercula* are slightly more ciliate than those of *T. filicaulis* (compare Figs. 3 and 4B), the difference is slight.

2. *Trichocolea floccosa* Herzog & R. Hatcher, n. sp.

Sterilis. Mediocris, pallide virens; caulis ad 1.2 mm. latus, 3–5 cm. longus, sine paraphylliis, pinnatus ad rarius bipinnatus; folia caulina approximata, oblique patula, subsymmetrica, ad 1 mm. longa, 1 mm. lata, limbo basali brevissimo, 1 cellula alto, folium ceterum quadrifidum, lobis validis lanceolatis, opposito-setosis, setulis simplicibus vel furcatis; cellulae disci 55 x 18  $\mu$ , cuticula striolata; amphigastria caulina symmetrica, ad 1 mm. longa, 0.7 mm. lata, quadrifida, lobis et setulis ut in folio.

## EXPLANATION OF FIGURES 47–59

FIGS. 47–59. *Trichocolea brevifissa* Steph. 47. Cross-section of a stem,  $\times 55$ . 48. Portion of a stem cross-section,  $\times 235$ . 49. Stem leaf,  $\times 55$ . 50. Stem underleaf,  $\times 55$ . 51. Branch leaf,  $\times 55$ . 52. Branch underleaf,  $\times 55$ . 53. Cells from the lamina of a leaf,  $\times 235$ . 54. Portion of a cilium,  $\times 235$ . 55. Cross-section of a stem,  $\times 55$ . 56. Portion of a stem cross-section,  $\times 235$ . 57. Male bract,  $\times 55$ . 58. Male bracteole,  $\times 55$ . 59. Portion of a stem showing leaf insertion, dorsal view,  $\times 10$ . FIGS. 47–48, drawn from a portion of *T. subquadrata* from Trinidad, collected by Crüger (G; FH); 49–59 from a portion of the original material from Brazil (G).





Plants in tufts, pale, yellowish-green: stems with leaves to 1.2 mm. wide, 3–5 cm. long, pinnate to irregularly bipinnate, stem in cross-section, oval to orbicular, 8–10 cells in diameter; cells of the medulla averaging  $24\ \mu$ , those of the cortex in a single layer, averaging  $18\ \mu$ ; cuticle thickened, striolate-papillose; paraphyllia absent; branches mostly 5–8 mm. long; rhizoids not seen: leaves approximate, spreading, nearly symmetrical, to 1 mm. long, 1 mm. wide, twice bifid nearly to the base into four nearly equal segments, the segments triangular in outline, ciliate with simple or branched cilia; lamina of the leaf one cell long, cells rectangular in outline, averaging  $55\ \mu$  long,  $18\ \mu$  wide; the cuticle striolate-papillose, cells of the cilia averaging  $110\ \mu$  long,  $10\ \mu$  wide: underleaves smaller than the leaves, to 1 mm. long, 0.7 mm. wide, twice bifid to three fourths, cilia similar to those of the leaf; branch leaves and underleaves similar to those of the stem but smaller: male and female inflorescence and sporophyte not seen. (Figs. 5–7).

Habitat: Not given.

The distinguishing characteristics of this species include its small size, its pinnate to irregularly bipinnate habit and its nearly symmetrical, deeply twice bifid leaves with a lamina only one cell long, and cells averaging  $55 \times 18\ \mu$ .

Distribution: Costa Rica: Santa Clara, W. R. Maxon, no. 8194, the original material (Hb. Herzog).

This species may be distinguished from *T. filicaulis* by its larger size, pinnate to irregularly bipinnate habit, and by its nearly symmetric, twice bifid leaves.

### 3. *TRICHOCOLEA SPRUCEI* Steph., Spec. Hepat. **4**: 59. 1909.

*Trichocolea gracillima* Spruce, Journ. Linn. Soc. Bot. **30**: 353. 1893. (not *T. gracillima* Austin).

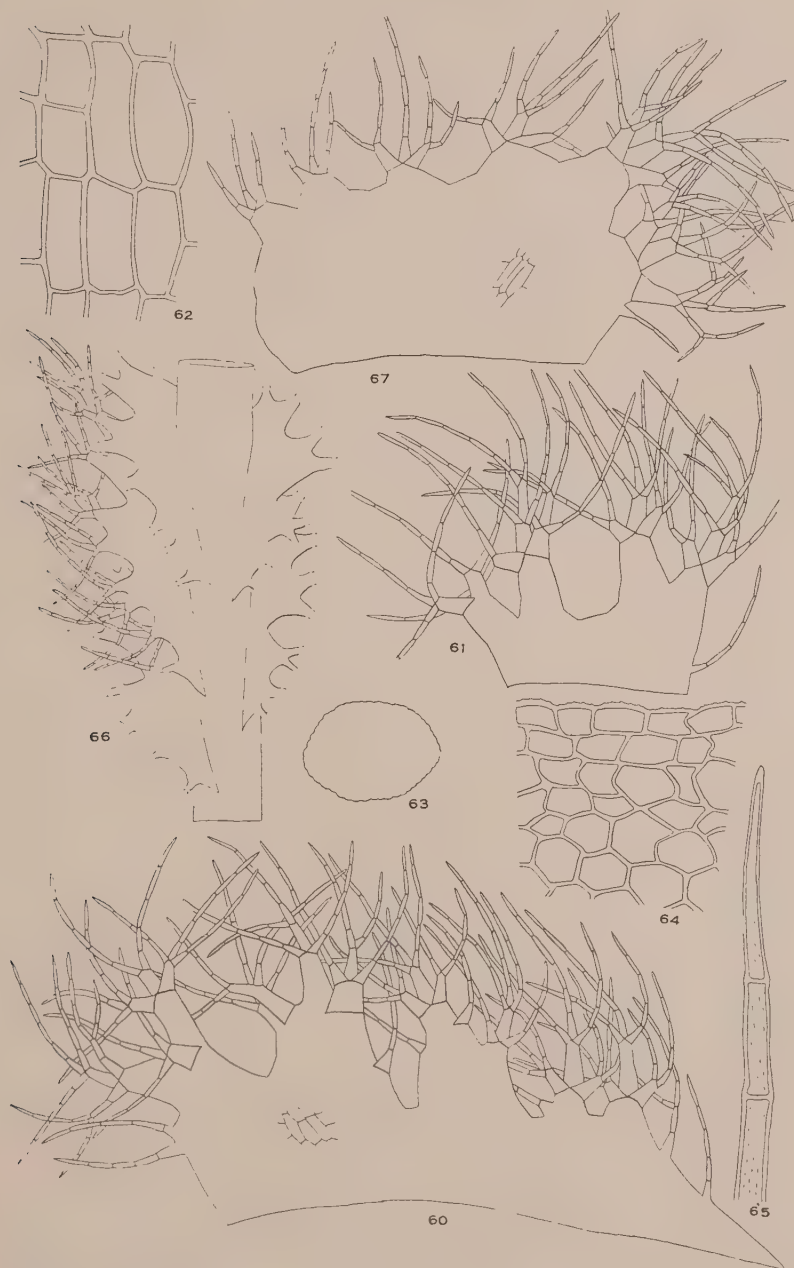
Plants in tufts, pale, greenish-white: stems with leaves to 1.2 mm. wide, 5 cm. long, simply pinnate, stem in cross-section, oval to orbicular, 8–10 cells in diameter; cells of the medulla averaging  $35\ \mu$ , those of the cortex in a single layer, averaging  $27\ \mu$ ; the cuticle thickened, striolate-papillose; paraphyllia absent, branches to 7 mm. long; rhizoids not seen: leaves approximate, spreading, nearly symmetrical, to 1 mm. long, 1.3 mm. wide, twice bifid to five-sixths into four nearly equal segments, the segments triangular in outline, ciliate with simple or branched cilia; lamina of the leaf 1–2 cells long, cells rectangular in outline, averaging  $91\ \mu$  long,  $29\ \mu$  wide, the cuticle striolate-papillose, cells of the cilia averaging  $120\ \mu$  long,  $10\ \mu$  wide: underleaves smaller

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#### EXPLANATION OF FIGURES 60–67

FIGS. 60–67. *Trichocolea Elliottii* Steph. 60. Stem leaf,  $\times 55$ . 61. Stem underleaf,  $\times 55$ . 62. Cells from the lamina of a leaf,  $\times 235$ . 63. Cross-section of a stem,  $\times 55$ . 64. Portion of a stem cross-section,  $\times 235$ . 65. Portion of a cilium,  $\times 235$ . 66. Portion of a stem showing leaf insertion, dorsal view,  $\times 15$ . 67. Male bract,  $\times 55$ . FIGS. 60–66, drawn from a portion of the original material from Dominica (G); FIG. 67 from the original material of *T. coalita* Steph. from Juan Fernandez (G).





than the leaves, to 0.8 mm. long, 0.8 mm. wide, twice bifid to five sixths into four or five segments, ciliate as in the leaves; branch leaves and underleaves similar to those of the stem but smaller: male and female inflorescence and sporophyte not seen. (Figs. 8-10).

Habitat: On trees.

The distinguishing characteristics of this species include its small size, its simply pinnate habit and its nearly symmetrical, deeply twice bifid leaves with a lamina 1-2 cells long, the cells averaging  $91 \times 29 \mu$ .

Distribution: Dominica: Mount Diablotin, Elliott, no. 684, the original material (Manch.).

*T. Sprucei* closely resembles *T. floccosa* in size of the plants and size and configuration of leaves. It may be distinguished from the latter by its simply pinnate habit and by the cells of the leaf lamina which, in *T. Sprucei*, average nearly twice the size of those of *T. floccosa*.

4. *TRICHOCOLEA FLACCIDA* (Spruce) Jack & Steph., Hedwigia **31**: 14. 1892.

*Leiomitra flaccida* Spruce, Trans. & Proc. Bot. Soc. [Edinburgh] **15**: 349. 1885.

*Trichocolea tomentosa* var. *canelensis* Spruce, ms., Hepat. Spruc. p.p.

*Trichocolea patula* Steph., Spec. Hepat. **4**: 57. 1909.

*Trichocolea inaequalis* Steph., op. cit. p. 58.

*Trichocolea Eggersiana* Steph., op. cit. p. 59.

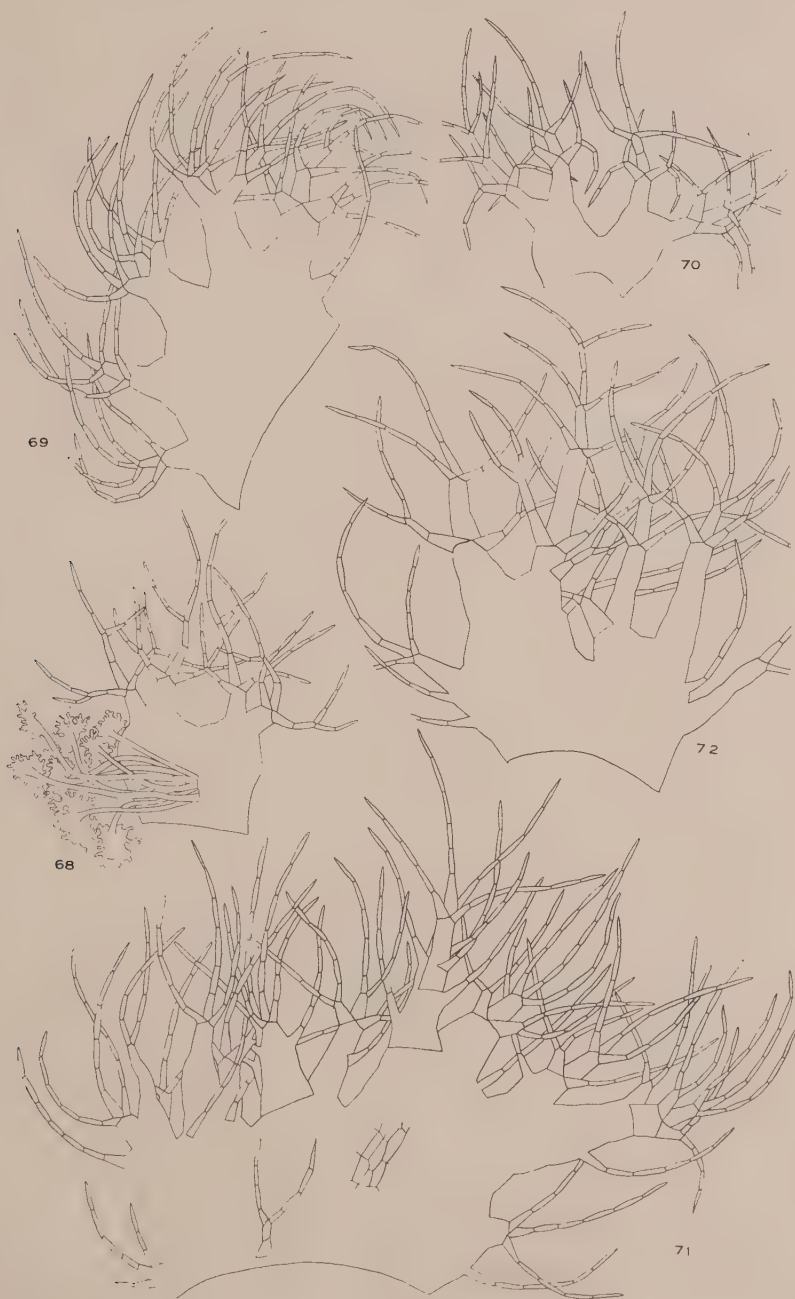
*Trichocolea Herzogii* Steph., Bibliotheca Bot. **87**: 230. 1916.

Plants in tufts, pale, yellowish-green: stems with leaves to 1 mm. wide, 4-8 cm. long, irregularly pinnate to bipinnate; stem in cross-section, orbicular to oval, 8-12 cells across; cells of the medulla averaging  $38 \mu$ , cells of the cortex in one layer, averaging  $28 \mu$ , cuticle thickened striolate-papillose; paraphyllia absent; rhizoid discs often developed on the lamina of underleaves, rhizoids when present arising in tufts, each rhizoid ending in a disc-shaped plate; branches mostly 5 mm. long: leaves distant to imbricated, spreading, asymmetrical, to 1.5 mm. long, 1 mm. wide, divided to one half into 4-5 unequal, often divided segments; the segments triangular in outline, the margins with a few long, simple or branched cilia; lamina 4-5 cells long, cells mostly rectangular in outline, averaging  $62 \mu$  long,  $19 \mu$  wide, the cuticle striolate-papillose: underleaves smaller, to 0.8 mm. long, 0.3 mm. wide, divided to one half into usually four segments, cilia similar to those of the leaf: branch leaves and underleaves similar to those of the stem but smaller: male inflorescence intercalary on a stem or branch, the bracts and bracteoles usually in 10 or more series; bracts concave, 1 mm. long, 1 mm. wide, divided into 5-6 segments; bracteoles similar to the underleaves; antheridia large, globose, borne singly, the stalk 12-14 cells long: female inflorescence and sporophyte not seen. (Figs. 11-40).

#### EXPLANATION OF FIGURES 68-72

FIGS. 68-72. *Trichocolea Elliottii* Steph. 68. Male bracteole showing rhizoids,  $\times 55$ . 69. Branch leaf,  $\times 55$ . 70. Branch underleaf,  $\times 55$ . 71. Innermost female bract,  $\times 55$ . 72. Innermost female bracteole,  $\times 55$ . FIG. 68, drawn from a portion of the original material of *T. coalita* Steph. from Juan Fernandez (G); FIGS. 69-72, from a portion of the original material from Dominica (G).





Habitat: On bark.

The distinguishing characteristics of this species are its asymmetrical leaves divided to one half into 4-5 usually sparsely ciliate segments with a lamina 4-5 cells long.

Distribution: Cuba; Sierra di Gavilanes, Leon & Luna, no. 6721, (NY).—Puerto Rico: without locality, Sintensis, no. 86, 95, cited by Stephani (1888).—Guadeloupe: without locality, L'Herminier, (NY); without locality, Marie, no. 143, cited by Bescherelle (1893, 185).—Dominica: without locality, Eggers, the original material of *T. patula*, (G); without locality, Elliott, the original material of *T. Eggersiana*, (G); Morne Couronne, Elliott, no. 218, cited by Spruce (1893, 353).—Guatemala: without locality or collector, as *T. inaequalis*, (G); Alta Verapaz, near Cobán, Türkheim, (NY).—Costa Rica: near La Palma, Maxon, (NY); Monte Torrecilla, Britton, Cowell, and Brown, no. 5685, (NY); Las Nubes, Standley, no. 33.068, 33.066, 38.184; La Hondura, Standley, no. 36.320, cited by Herzog (1938, 30) as *T. patula*.—Colombia: Bogotá, Weir, (NY).—Ecuador: Canelos, cited by Spruce as the original of *L. flaccida* (1885, 349); Canelos, Spruce, Hepat. Spruc., as *T. (Leiomitra) tomentosa* var. *canelensis* Spruce, ms., p.p., (NY);—Peru: Mt. Campana, Spruce, Hepat. Spruc., as *T. (Leiomitra) flaccida*, (NY);—Bolivia: without locality, Herzog, no. 4297, the original material of *T. Herzogii*, (G); Sillar, Herzog, no. 2776, cited by Herzog (1916, 230).

*Trichocolea flaccida* is a highly variable species and a number of taxa fall within the limits of its variation and are here reduced to synonymy. The plants are generally rather small, and irregularly pinnate to bipinnate with the leaves asymmetrical and deeply divided into 4-5 sparsely ciliate segments.

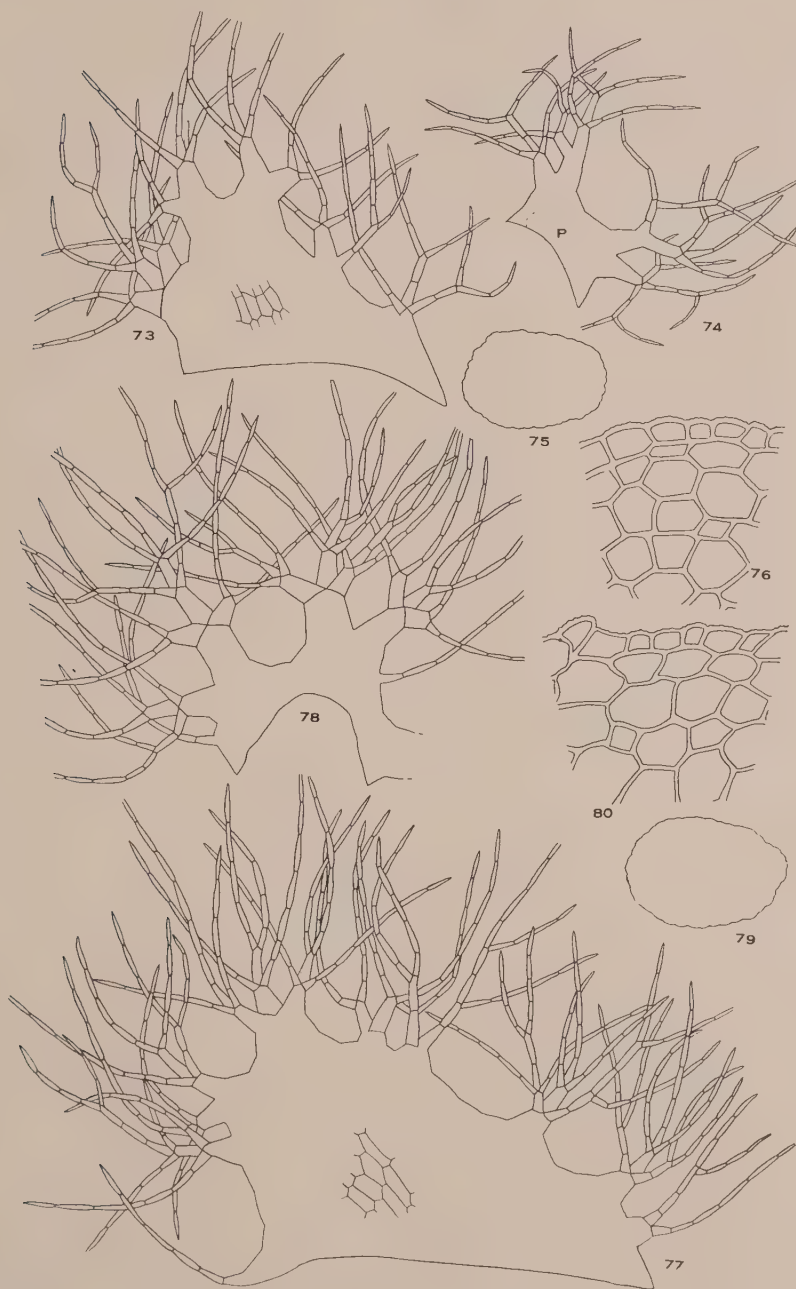
The original material of *T. patula* from Dominica differs only in that the underleaves are somewhat more deeply divided and have longer, more slender segments than those of *T. flaccida*. (Compare Figs. 12A and 26). In *T. inaequalis* from Guatemala (probably the original material), the difference is again only in the underleaves which are broader and more densely ciliate than those of *T. flaccida* as is seen in a comparison of Figures 12A and 38. In *T. Eggersiana* from Dominica, the leaves are more densely ciliate and the underleaves somewhat more deeply divided. (Compare Figs. 11A with 33 and 12A with 34). In *T. Herzogii* from Bolivia, also, the underleaves are more deeply divided and more densely ciliate. (Compare Figs. 12A with 22).

The situation with regard to *T. (Leiomitra) tomentosa* var. *canelensis* from Ecuador, distributed in the *Hepaticae Spruceanae*, is confusing in

#### EXPLANATION OF FIGURES 73-80

FIGS. 73-80. *Trichocolea Elliottii* Steph. 73. Stem leaf,  $\times 55$ . 74. Stem underleaf with rhizoid pad (P),  $\times 55$ . 75. Cross-section of a stem,  $\times 55$ . 76. Portion of a stem cross-section,  $\times 235$ . 77. Stem leaf,  $\times 55$ . 78. Stem underleaf,  $\times 55$ . 79. Cross-section of a stem,  $\times 55$ . 80. Portion of a stem cross-section,  $\times 235$ . FIGS. 73-76, drawn from a portion of the original material of *T. coalita* from Juan Fernandez (G); FIGS. 77-80, from a portion of the original material of *T. opposita* Steph. from Juan Fernandez (G).





that the material is a mixture of two species. One of these is *T. tomentosa* and it is assumed that the varietal name was applied to the other species. Although this latter material has a growth habit similar to that of *T. tomentosa*, it differs from that species in that its leaves and underleaves are similar to those of *T. flaccida*. The leaves are divided into only four short, sparsely ciliate segments and have a narrower insertion than those of *T. flaccida* and the underleaves are more deeply divided. (Compare Figs. 11A with 29 and 12A with 30).

*T. flaccida* may be separated from *T. Sprucei*, a species of similar size, by its asymmetric leaves with a lamina 4–5 cells long. The leaves of *T. Sprucei* are nearly symmetrical and the lamina is only 1–2 cells long.

5. *TRICHOCOLEA BREVIFISSA* Steph., Rio de Janeiro, Mus. Nac. Arch. **13**: 114. 1905.

*Trichocolea subquadrata* Steph., Spec. Hepat. **4**: 53. 1909.

*Trichocolea cubensis* Steph., op. cit. p. 54.

Plants in tufts, pale, yellowish-green: stems with leaves to 2 mm. wide, 3–4 cm. long, pinnate to bipinnate; stem in cross-section, oval to orbicular, to 16 cells in diameter; cells of the medulla averaging 24  $\mu$ , cells of the cortex in 1–2 layers, averaging 18  $\mu$ , cuticle thickened, striolate-papillose; paraphyllia absent; branches mostly 3–4 mm. long; rhizoids not seen: leaves distant to approximate, spreading, asymmetrical, to 1 mm. long, 1.5 mm. wide, divided to one fourth into 4–5 short, unequal segments; the segment triangular in outline, sparsely ciliate with simple or branched cilia; lamina 8–14 cells long, the cells rectangular in outline, averaging 58  $\mu$  long, 26  $\mu$  wide; cells of the cilia averaging 83  $\mu$  long, 16  $\mu$  wide; the cuticle striolate-papillose: underleaves smaller, to 0.7 mm. long, 1 mm. wide, deeply divided into usually 4 segments, cilia similar to those of the leaves, a rhizoid disc often present; branch leaves and underleaves similar to those of the stem, but smaller: male inflorescence intercalary or terminal on the stem or branch, bracts and bracteoles in 5 or more series; bracts concave, to 0.8 mm. long, 1.3 mm. wide, divided to one third into 6–7 short segments; bracteoles similar to the underleaves; antheridia large, globose, borne singly, the stalk 14–16 cells long: female inflorescence and sporophyte not seen. (Figs. 41–59).

Habitat: On bark and leaves.

The distinguishing characteristics of this species are the closely imbricated leaves with a lamina 8–14 cells long, and with 4–5 short, unequal segments.

Distribution: Cuba: without locality, Wright, the original material

#### EXPLANATION OF FIGURES 81–87

FIGS. 81–87. *Trichocolea paraphyllina* (Spruce) Steph. 81. Stem leaf,  $\times 40$ . 82. Stem underleaf,  $\times 40$ . 83. Branch leaf,  $\times 40$ . 84. Branch underleaf with rhizoids (R),  $\times 40$ . 85. Cells from the lamina of a leaf,  $\times 235$ . 86. Portion of a cilium,  $\times 235$ . 87. Portion of a stem showing leaf insertion and paraphyllia, dorsal view,  $\times 15$ . FIGS. 81–87, drawn from material of *L. paraphyllina* collected and named by Spruce from Mt. Tunguragua, Ecuador (NY).





of *T. cubensis*, (G).—Jamaica: without locality or collector, (NY); without locality, cited by Pearson (1931) as *T. cubensis*.—Puerto Rico: without locality, Sintensis, no. 84, as *T. subquadrata*, (G); Mt. Torrecilla, Britton, Cowell, & Brown, (NY); near Los Picachos, Pagán, no. 322, (FH).—Martinique: without locality, Perrotet, no. 36, as *T. subquadrata*, (G).—Trinidad: without locality, Crüger, as *T. subquadrata*, (G; FH); Mt. Tocuche, Britton, Coker, & Rowland, no. 1483, 1475, (NY).—Brazil: without locality, Ule, the original material, (G); Minas Geraes, the original material of *T. subquadrata*, cited by Stephani (1900, 54).

The vegetative characters of *T. brevifissa* are quite distinct and the leaf with its long lamina and short segments will serve to separate it from other species. The original material of *T. cubensis* collected by Wright in Cuba has similar leaves, but the cilia are usually 4 and sometimes 5 cells in length while those of the original material of *T. brevifissa* are usually 3 and sometimes 4 cells long. Since there is so much variation in this character on even one stem, it does not seem to be of sufficient magnitude to merit specific distinction, and *T. cubensis* is therefore reduced to synonymy.

The original material of *T. subquadrata* from Brazil was not available, and material collected by Crüger in Trinidad and determined by Stephani, from the Stephani Collections in the Farlow Herbarium and from the Conservatoire et Jardin Botaniques, Geneva, was considered authentic. These plants could not be differentiated from *T. brevifissa*.

*T. brevifissa* differs from *T. filicaulis* in its larger size and in the much larger lamina of the leaf. The lamina of the leaf of the latter species is only one to two cells long. It differs from *T. flaccida* in having a longer lamina and shorter segments and cilia. This is seen in a comparison of Figures 41, 45, and 49 with Figures 11A, 21, 25, 29, 33, and 37.

#### 6. *TRICHOCOLEA ELLIOTTII* Steph., Spec. Hepat. 4: 55. 1909.

*Trichocolea opposita* Steph., Svenska Vetensk. Akad. Handl. 46(9): 77. 1911.

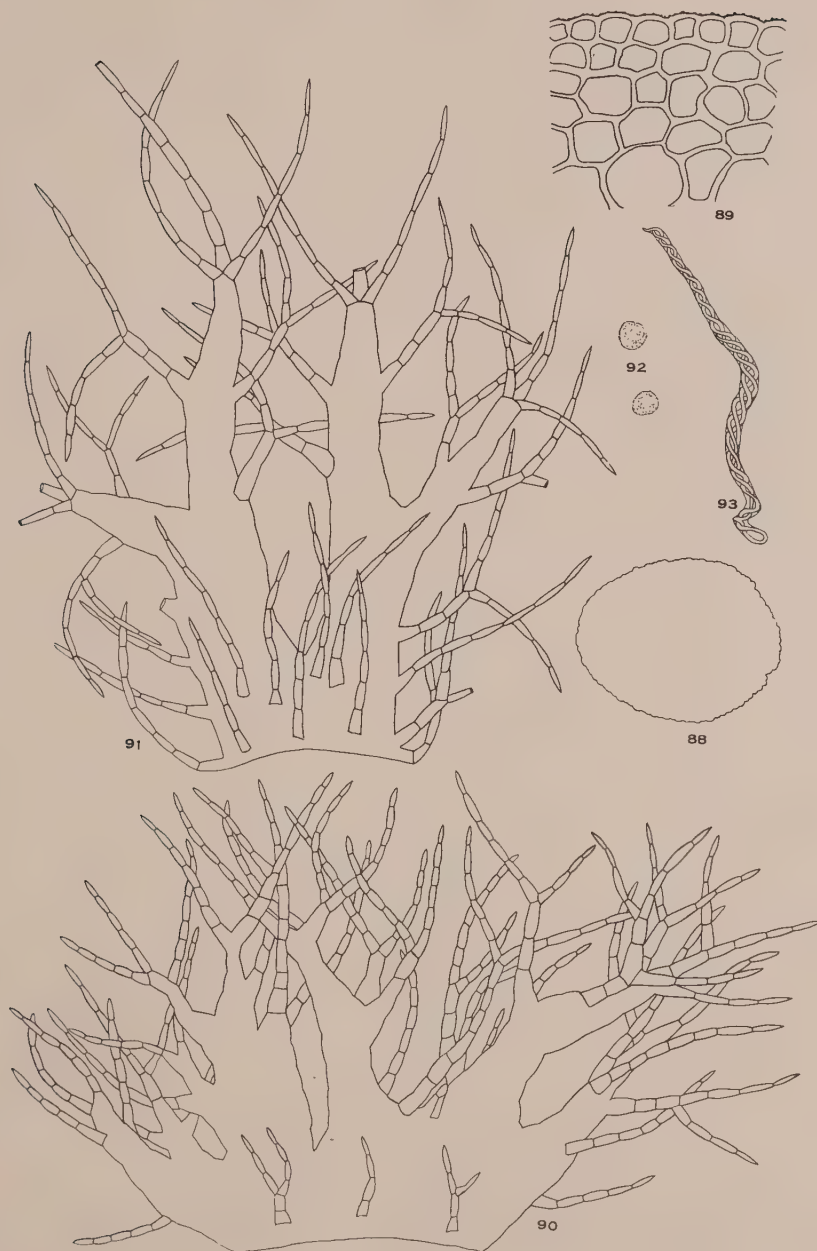
*Trichocolea coalita* Steph., loc. cit. 1911.

Plants large, in tufts, pale, yellowish-green: stems with leaves to 2 mm. wide, 6–7 cm. long, pinnate; stem in cross-section, oval to orbicular, 12–14 cells in diameter; cells of the medulla averaging 31  $\mu$ , cells of the cortex in one to two layers, averaging 24  $\mu$ , cuticle thickened, striolate-papillose; paraphyllia absent; branches mostly 4–5 mm. long; rhizoids, when present, from the lamina of a branch underleaf or a male bracteole, each with a deeply lobed disc at the tip: leaves closely imbricated, spreading, asymmetrical, attached in an oblique line, to 1.3 mm. long, 2 mm. wide, divided to approximately one half into

#### EXPLANATION OF FIGURES 88–93

FIGS. 88–93. *Trichocolea paraphyllina* (Spruce) Steph. 88. Cross-section of a stem,  $\times 55$ . 89. Portion of a stem cross-section,  $\times 235$ . 90. Female bract,  $\times 40$ . 91. Female bracteole,  $\times 40$ . 92. Spores,  $\times 235$ . 93. Elater,  $\times 235$ . FIGS. 88–93, drawn from a portion of the original material from Mt. Guayrapata, Ecuador, (NY).





5-6 unequal, often divided segments; the segments triangular in outline, densely ciliate with simple or branched cilia; lamina to 6 cells long, the cells mostly rectangular in outline, averaging  $62\ \mu$  long,  $31\ \mu$  wide, cells of the cilia averaging  $96\ \mu$  long,  $20\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, symmetrical, to 1 mm. long, 1 mm. wide, deeply divided into usually four segments, ciliate as in the leaves: branch leaves and underleaves similar to those of the stem but smaller: male inflorescence intercalary on a branch, the bracts and bracteoles in usually 8 or more series; bracts concave, larger than the branch leaves, to 1.2 mm. long, 2 mm. wide, divided to one third into 5-6 short segments, bracteoles similar to the branch underleaves but larger, with a broader lamina, to 1 mm. long, 0.5 mm. wide; antheridia large, globose, borne in pairs, the stalk 8-10 cells long: female inflorescence terminal on a main stem or branch, the bracts and bracteoles in three series, the innermost series the largest; the bracts subsymmetrical, to 2 mm. long, 2 mm. wide, divided to one half into 8-10 unequal, often divided segments, ciliate as in the leaves, lamina 6-7 cells long, the cells averaging  $84\ \mu$  long,  $25\ \mu$  wide; bracteoles symmetrical, to 1.3 mm. long, 1.2 mm. wide, deeply divided into 4-6 segments, the lamina to 6 cells long: sporophyte not seen. (Figs. 60-80).

Habitat: On soil and on the bark of trees.

The distinguishing characteristics of this species include its large size and the asymmetrical leaves which are somewhat decurrent and divided into 5-6 long segments from a lamina to 6 cells long.

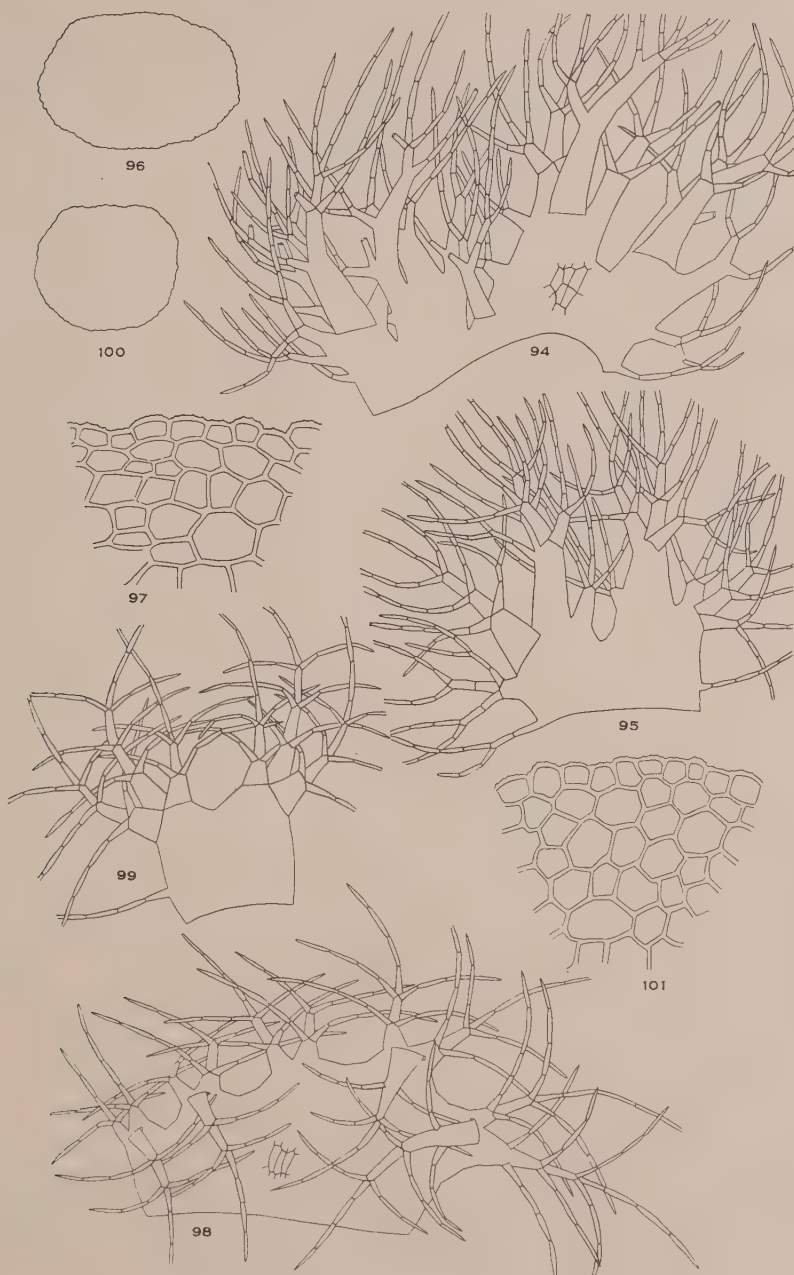
Distribution: Cuba: Loma del Gato, Leon, Clement, & Roco, (NY).—Jamaica: John Crow Peak, Maxon & Killip, no. 983, (NY); Blue Mt. Peak, Maxon & Killip, no. 1180, (NY).—Guadeloupe: without locality, L'Herminier, (NY).—Dominica: without locality, Elliott, the original material, (G).—Martinique: without locality, Dusén, (NY).—St. Vincent: without locality, Smith, no. 1445, as *Leiomitra tomentosa*, (FH).—Juan Fernandez: without locality, Skottsberg, no. 135, the original material of *T. opposita*, (G); without locality, Skottsberg, no. 637, the original material of *T. coalita*, (G).

An examination of the original material of both *T. opposita* and *T. coalita* revealed no distinctive differences which would serve to distinguish these from the original material of *T. Elliottii*. Stephani stated, in his original description of *T. opposita*, that the leaves were opposite, and apparently based his specific distinction upon this character. On close examination, however, the leaves were found to be alternate as in the other species of the genus.

The plants of *T. coalita*, although somewhat smaller than those of

#### EXPLANATION OF FIGURES 94-101

FIGS. 94-97. *Trichocolea paraphyllina* (Spruce) Steph. 94. Stem leaf,  $\times 55$ . 95. Stem underleaf,  $\times 55$ . 96. Cross-section of a stem,  $\times 55$ . 97. Portion of a stem cross-section,  $\times 235$ . FIGS. 98-101. *Trichocolea elegans* Lehmann. 98. Stem leaf,  $\times 55$ . 99. Stem underleaf,  $\times 55$ . 100. Cross-section of a stem,  $\times 55$ . 101. Portion of a stem cross-section,  $\times 235$ . FIGS. 94-97, drawn from a portion of the original material of *T. difficilis* Steph. from Bolivia (G); FIGS. 98-101, from a portion of the original material of *T. decrescens* Steph. from Patagonia (G).





the original of *T. Elliottii*, are otherwise indistinguishable. (Compare Figs. 60 and 73). The presence of a rhizoid pad on the lamina of the underleaf in *T. coalita* (see Fig. 74, p) does not constitute a reliable character for the separation of species since it is of sporadic occurrence and, when present, is usually not developed on all of the underleaves of a stem.

7. *TRICHOCOLEA PARAPHYLLINA* (Spruce) Steph., Spec. Hepat. **4**: 58. 1909.

*Leiomitra paraphyllina* Spruce, Trans. & Proc. Bot. Soc. [Edinburgh] **15**: 350. 1885.  
*Trichocolea difficilis* Steph., Bibliotheca Bot. **87**: 230. 1916.

Plants large, in tufts, pale, yellowish-green: stems with leaves to 2 mm. wide, 6–8 cm. long, irregularly pinnate to bipinnate; stem in cross-section, oval to orbicular, 16–20 cells in diameter; cells of the medulla averaging  $34\ \mu$ , cells of the cortex in 2–3 layers, averaging  $22\ \mu$ , cuticle thickened, striolate-papillose; paraphyllia usually numerous except on the ventral side, uniseriate, 5–8 cells long, occasionally branched; primary branches mostly 1 cm. long; rhizoids, when present, arising in tufts from the lamina of underleaves, hyaline, often fused and terminating in a disc-shaped plate: leaves distant to approximate, spreading, asymmetrical, to 1.5 mm. long, 2.5 mm. wide, divided to one half or more into 4–6 unequal, often divided segments; the segment triangular in outline, ciliate with long, simple or branched cilia; lamina 6–8 cells long, cells long rectangular in outline, averaging  $115\ \mu$  long,  $32\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, to 1.5 mm. long, 1 mm. wide, divided to three fourths into 5–6 unequal often divided segments, cilia similar to those of the leaf: branch leaves and underleaves similar to those of the stem but smaller and usually with fewer segments: female inflorescence terminal on a main stem or branch, bracts and bracteoles in three series, symmetrical, bracts to 2 mm. long, 2 mm. wide, deeply divided into 5–7 unequal, often divided segments, cells of the lamina averaging  $74\ \mu$  long,  $31\ \mu$  wide; ciliate as in the leaves and with scattered superficial cilia on the lamina; bracteoles to 2 mm. long, 1.3 mm. wide, deeply divided into usually 4 ciliate segments, with numerous superficial cilia on the lamina: sporophyte surrounded by a spherical, sparsely ciliate coelocaul; sporangium large, dark reddish-brown; elaters to  $300\ \mu$  long,  $9\ \mu$  wide, 3-spiraled, with tapering, pointed ends; spores  $30\text{--}35\ \mu$ , minutely punctate. (Figs. 81–97).

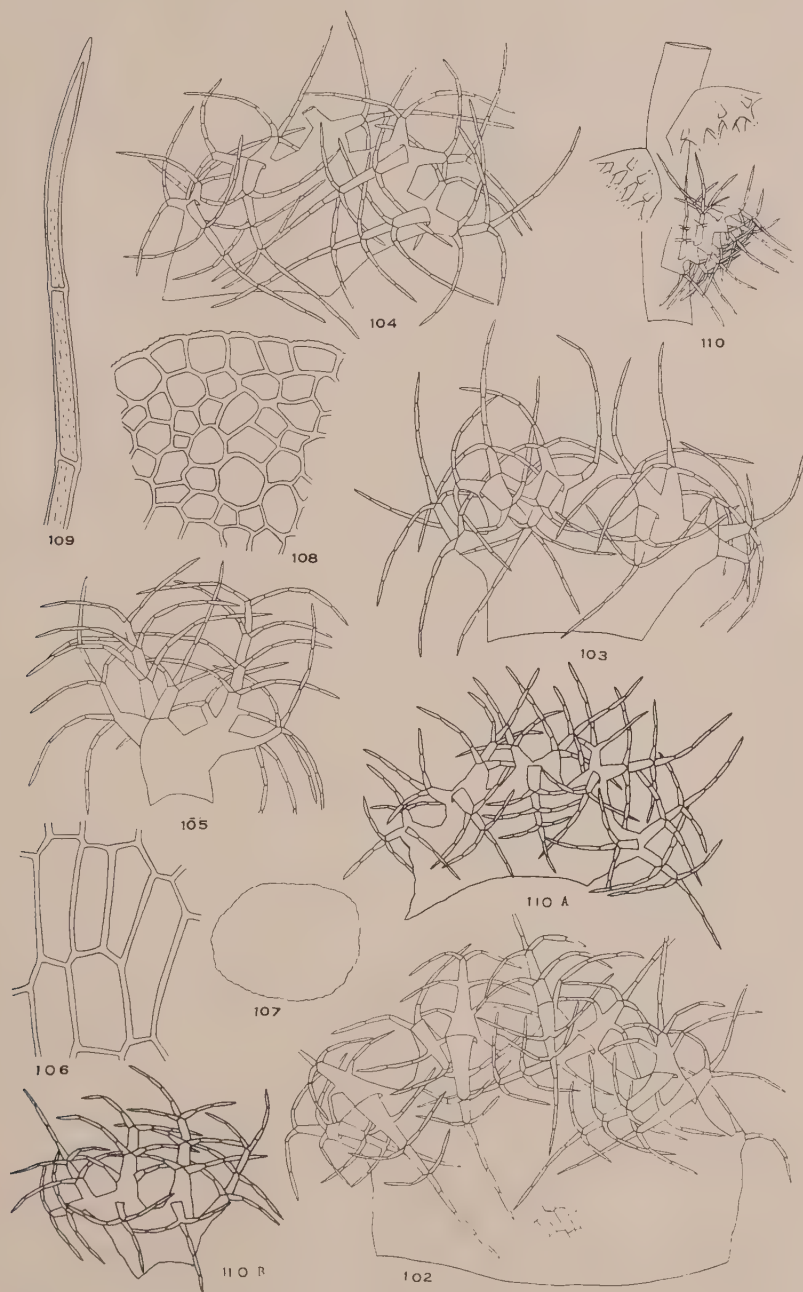
Habitat: On bark.

The distinguishing characteristics of this species include its large

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EXPLANATION OF FIGURES 102–110

FIGS. 102–110. *Trichocolea elegans* Lehmann. 102. Stem leaf,  $\times 55$ . 103. Stem underleaf,  $\times 55$ . 104. Branch leaf,  $\times 55$ . 105. Branch underleaf,  $\times 55$ . 106. Cells from the lamina of a leaf,  $\times 235$ . 107. Cross-section of a stem,  $\times 55$ . 108. Portion of a stem cross-section,  $\times 235$ . 109. Portion of a cilium,  $\times 235$ . 110. Portion of a stem showing leaf insertion, dorsal view,  $\times 10$ . 110A. Stem leaf,  $\times 55$ . 110B. Stem underleaf,  $\times 55$ . FIGS. 102–110, drawn from a portion of the original material of *T. verticillata* Steph. from Chile (NY); FIGS. 110A and 110B, from a portion of the original material from Valdivia, Chile (NY).



size, the irregularly pinnate to bipinnate branching habit, the numerous paraphyllia on the stem, and the asymmetric leaves divided to one half or more into 4-6 unequal segments.

Distribution: Jamaica: John Crow Peak, Britton, (NY); same locality, Underwood, no. 212, (NY).—Guadeloupe: without locality, Dusén, (NY).—Martinique, without locality, Dusén (NY).—Mexico: Puebla, near Honey Station, Pringle, no. 15332, as *T. robusta* (FH).—Colombia: without locality, Wier (NY).—Ecuador: Mt. Tunguragua, Spruce, as *Leiomitra paraphyllina*, (NY); Mt. Guayrapata, Spruce, the original material (NY); Antombos, cited by Spruce (1885, 350).—Bolivia: without locality, Herzog, no. 4331, the original material of *T. difficilis* (G).

The original material of *T. difficilis* showed no marked differences which would separate the species from *T. paraphyllina*. In the original description of *T. difficilis*, Stephani did not mention the presence of paraphyllia on the stem. These are conspicuous on the stems of the original material although they are not as abundantly produced as in *T. paraphyllina* collected by Spruce on Mt. Tunguragua and figured here. The leaves of the two are not essentially different as is to be seen in a comparison of Figures 81 and 94.

*T. paraphyllina* may be readily distinguished from *T. Elliottii*, which it superficially resembles, by the presence of numerous paraphyllia on its stems, since in *T. Elliottii* there are no paraphyllia. The only other American species bearing paraphyllia on the stems are *T. robusta* and *T. tomentella* and the differences between these are discussed under the latter species.

#### 8. TRICHOCOLEA ELEGANS Lehmann, Pugillus 10: 8. 1875.

*Trichocolea verticillata* Steph., Bihang K. Svenska Vet. Akad. Handl. 26(6): 57. 1900.

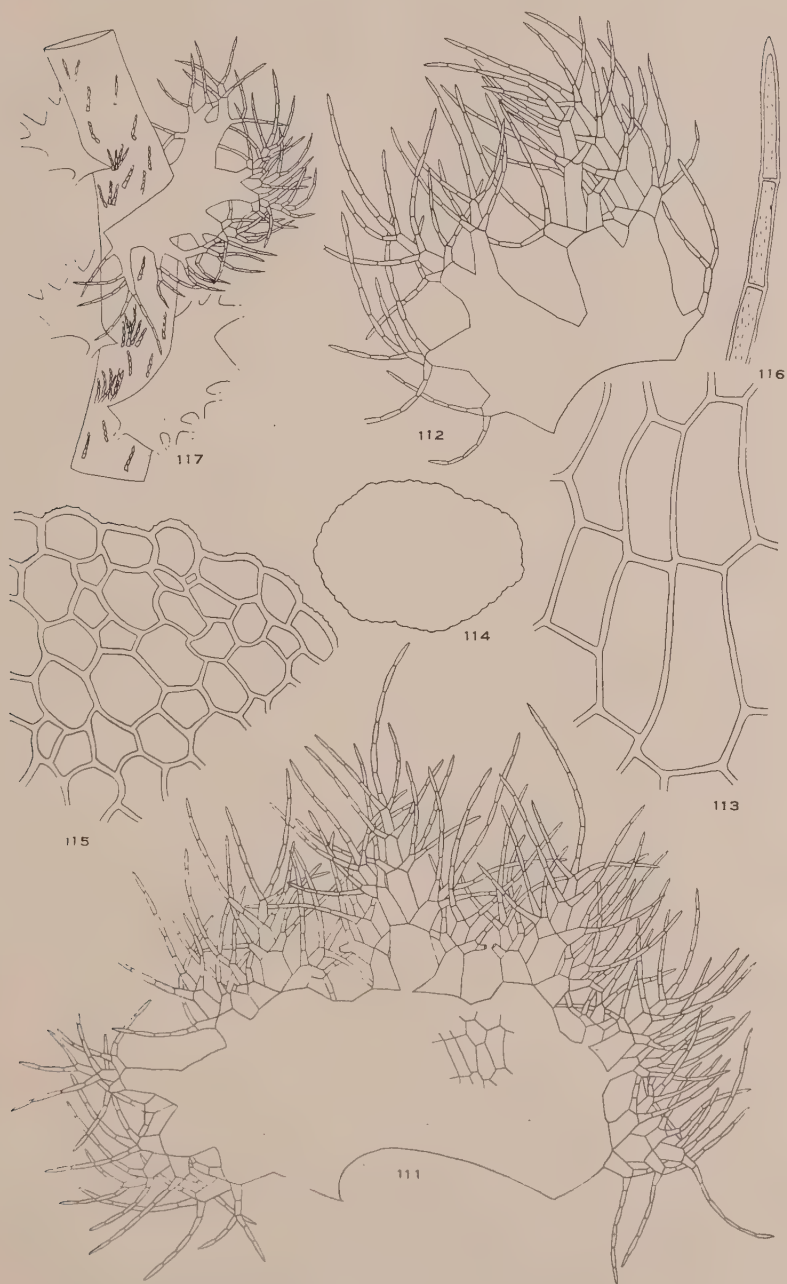
*Trichocolea decrescens* Steph., Svenska Vet. Akad. Handl. 46(9): 77. 1911.

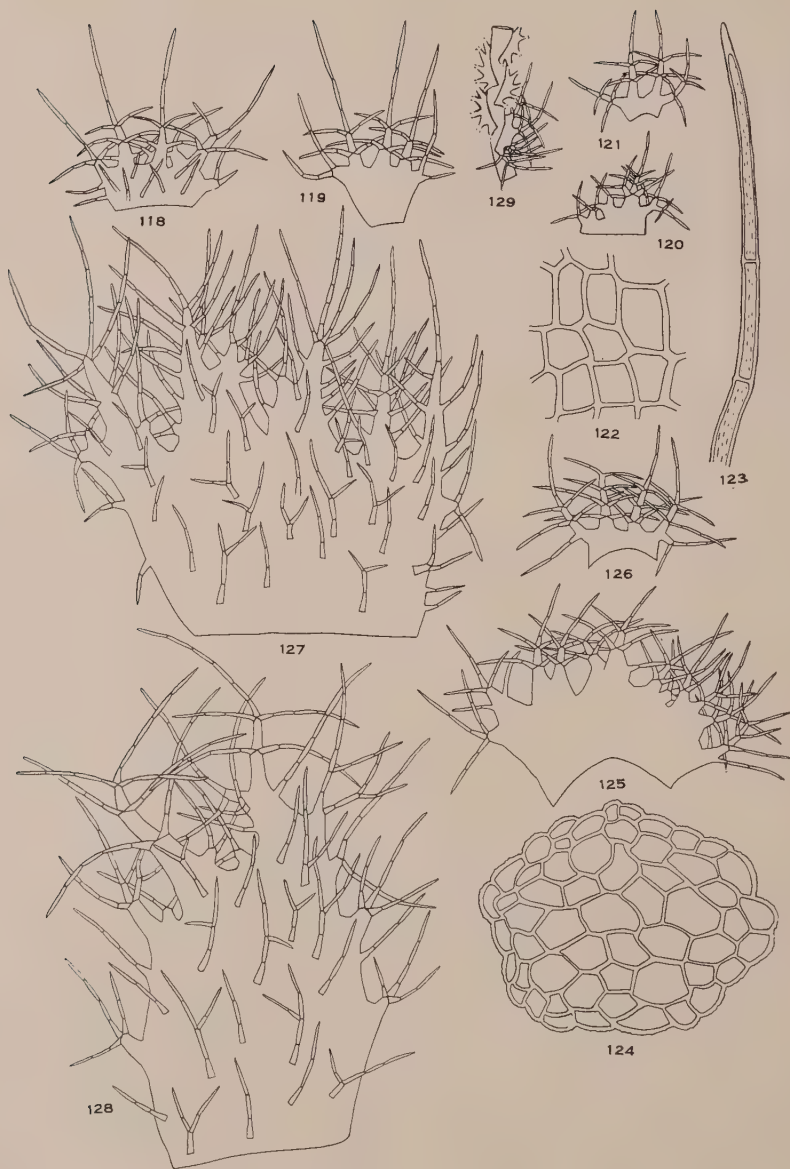
Plants in tufts or scattered among other bryophytes, pale, yellowish-green: stems with leaves to 2 mm. wide, 5 cm. long, pinnate to bipinnate; stems in cross-section, oval to orbicular, to 16 cells in diameter; cells of the medulla averaging 25  $\mu$ , cells of the cortex in 1-2 layers, averaging 19  $\mu$ , cuticle thickened, striolate-papillose; branches mostly 4-5 mm. long; rhizoids not seen: leaves distant to approximate, spreading, asymmetrical to subsymmetrical, scarcely to rather long decurrent dorsally, to 1 mm. long, 1.5 mm. wide, divided to one half into usually 5 bifid to trifid segments, with one of the divisions of a segment bent at a right angle to the lamina; the segment divisions narrowly triangular in outline, ciliate with long, mostly simple, recurved cilia, cells mostly

#### EXPLANATION OF FIGURES 111-117

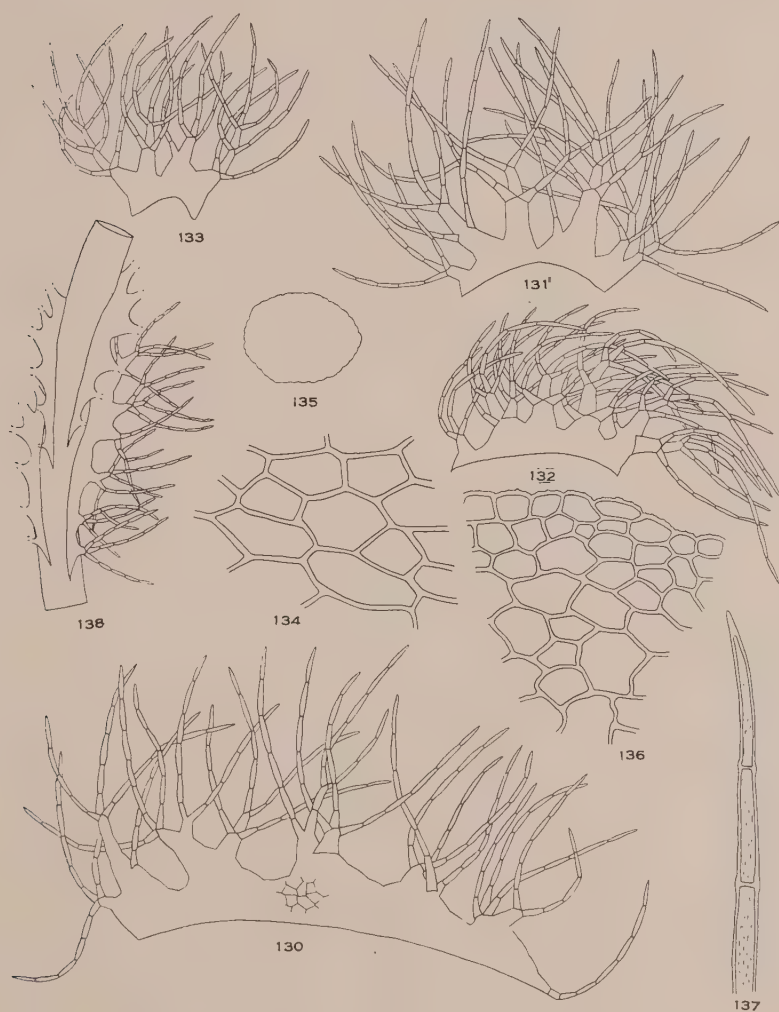
FIGS. 111-117. *Trichocolea robusta* Steph. 111. Stem leaf,  $\times 55$ . 112. Stem underleaf,  $\times 55$ . 113. Cells from the lamina of a leaf,  $\times 235$ . 114. Cross-section of a stem,  $\times 55$ . 115. Portion of a stem cross-section,  $\times 235$ . 116. Portion of a cilium,  $\times 235$ . 117. Portion of a stem showing leaf insertion and paraphyllia, dorsal view,  $\times 12$ . FIGS. 111-117, drawn from a portion of the original material from Colombia (G).







FIGS. 118-129. *Trichocolea argentea* Herzog. 118. Stem leaf,  $\times 55$ . 119. Stem underleaf,  $\times 55$ . 120. Branch leaf,  $\times 55$ . 121. Branch underleaf,  $\times 55$ . 122. Cells from the lamina of a leaf,  $\times 235$ . 123. Portion of a cilium,  $\times 235$ . 124. Cross-section of a stem,  $\times 235$ . 125. Male bract,  $\times 55$ . 126. Male bracteole,  $\times 55$ . 127. Female bract of the innermost series,  $\times 55$ . 128. Innermost female bracteole,  $\times 55$ . 129. Portion of a stem showing leaf insertion, dorsal view,  $\times 10$ . FIGS. 118-129, drawn from a portion of the type material from Brazil (Hb. Herzog).



FIGS. 130-138. *Trichocolea Uleana* Steph. 130. Stem leaf,  $\times 55$ . 131. Stem underleaf,  $\times 55$ . 132. Branch leaf,  $\times 55$ . 133. Branch underleaf,  $\times 55$ . 134. Cells from the lamina of a leaf,  $\times 235$ . 135. Cross-section of a stem,  $\times 55$ . 136. Portion of a stem cross-section,  $\times 235$ . 137. Portion of a cilium,  $\times 235$ . 138. Portion of a stem showing leaf insertion, dorsal view,  $\times 12$ . FIGS. 130-138, drawn from a portion of the original material from Brazil (G).



rectangular in outline, averaging  $64\ \mu$  long,  $25\ \mu$  wide; cells of the cilia averaging  $95\ \mu$  long,  $9\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, symmetrical, to 0.8 mm. long, 1 mm. wide, divided to one half into 2 groups of usually 3 divisions each, ciliate as in the leaves: branch leaves and underleaves similar to those of the stem but smaller: male and female inflorescence and sporophyte not seen. (Figs. 98–110).

Habitat: On soil among other bryophytes.

The distinguishing characters of this species include the leaves, divided to one half into usually 5 bifid to trifid segments with one of the divisions of a segment bent at a right angle to the lamina, and the recurved cilia.

Distribution: Juan Fernandez: Masatierra, Skottsberg, no. 137, as *T. decrescens* (G); same locality, Skottsberg, no. 375, 386, 385, and 384, (NY).—Desolation Island: Puerto Augusto, Dusén, no. 391, (G).—Chile: Valdivia, Lechler, the original material, (NY); same locality, Hahn, (G); without locality, Dusén, the original of *T. verticillata*, (NY); Corral, Kräuse, (G); same locality, Thaxter, no. 32, 132, (NY); Puerto Varas, Gertrud & Hosseus, no. 297, (NY).—Argentina: near Lake Nahuelhuapi, Dusén, (NY).—Patagonia: without locality, Dusén, (NY); Puerto Bueno, Dusén, no. 52, (G); Cal. Rayo, Skottsberg, no. 587, the original of *T. decrescens*, (G).

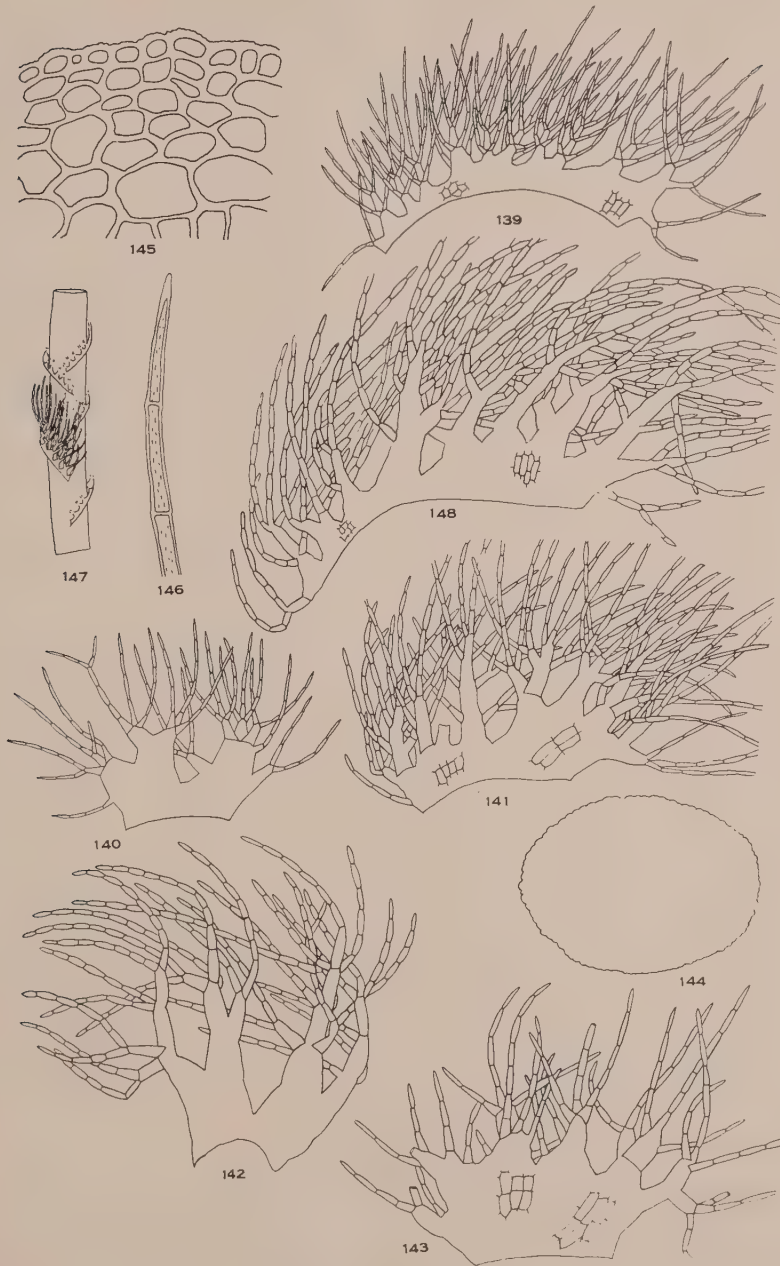
The original material of both *T. verticillata* and *T. decrescens* is essentially similar to that of *T. elegans*. Both are larger than *T. elegans* and *T. decrescens* has a more nearly symmetrical leaf, but these variations are not sufficient to keep the three as distinct species and *T. verticillata* and *T. decrescens* are therefore reduced to synonymy.

#### 9. *TRICHOCOLEA ROBUSTA* Steph., Spec. Hepat. 4: 58. 1909.

Plants large, in tufts, pale, yellowish-green: stems with leaves to 3 mm. wide, 5–8 cm. long, irregularly pinnate to bipinnate; stem in cross-section, oval, to 15 cells in diameter; cells of the medulla averaging  $35\ \mu$ , cells of the cortex in 1–2 layers, averaging  $24\ \mu$ , cuticle thickened, striolate-papillose; paraphyllia sparse, uniseriate, 5–8 cells long, occasionally branched, often occurring in clusters; branches to 1 cm. long; rhizoids not seen: leaves distant to approximate, spreading, more or less symmetrical, to 1.5 mm. long, 2.8 mm. wide, divided to one half into 6–8 unequal, divided segments; the divisions opposite or whorled, triangular in outline, very densely ciliate with simple or branched cilia; lamina to 7 cells long, the cells mostly long rectangular in outline, averaging  $80\ \mu$  long,  $36\ \mu$  wide; cells of the cilia averaging  $83\ \mu$  long,

#### EXPLANATION OF FIGURES 139–148

FIGS. 139–148. *Trichocolea tomentosa* (Sw.) Gottsche. 139. Stem leaf,  $\times 55$ . 140. Stem underleaf,  $\times 55$ . 141. Branch leaf,  $\times 55$ . 142. Branch underleaf,  $\times 55$ . 143. Male bract,  $\times 55$ . 144. Cross-section of a stem,  $\times 55$ . 145. Portion of a stem cross-section,  $\times 235$ . 146. Portion of a cilium,  $\times 235$ . 147. Portion of a stem showing leaf insertion, dorsal view,  $\times 10$ . 148. Stem leaf,  $\times 55$ . FIGS. 139–140, drawn from a portion of the original material from Jamaica (S-PA); FIGS. 141–148, from a portion of the original material of *L. sphagnoides* Spruce from Ecuador (NY).



12  $\mu$  wide; the cuticle striolate-papillose: underleaves smaller, symmetrical, to 1 mm. long, 1 mm. wide, deeply bifid and divided into usually 4-5 often divided segments, ciliate as in the leaves: branch leaves and underleaves similar to those of the stem, but smaller and with fewer segments: male and female inflorescence and sporophyte not seen. (Figs. 111-117).

Habitat: On bark.

The distinguishing characters of this species include its large size, the stem paraphyllia, and the leaves with 6-8 very densely ciliate segments.

Distribution: Colombia: Prov. Antioquia, Paramo de Sonson, Jack, the original material, (G).

*T. robusta* can be separated readily from *T. paraphyllina* which also has stem paraphyllia, by the larger number of densely ciliate segments of its leaves. (Compare Figs. 111 and 81). *T. tomentella* also has stem paraphyllia but it can be distinguished from *T. robusta* by its regularly bi-tripinnate branching since *T. robusta* is at most only irregularly branched. The leaves of the two are also very different. (Compare Figs. 111 and 169).

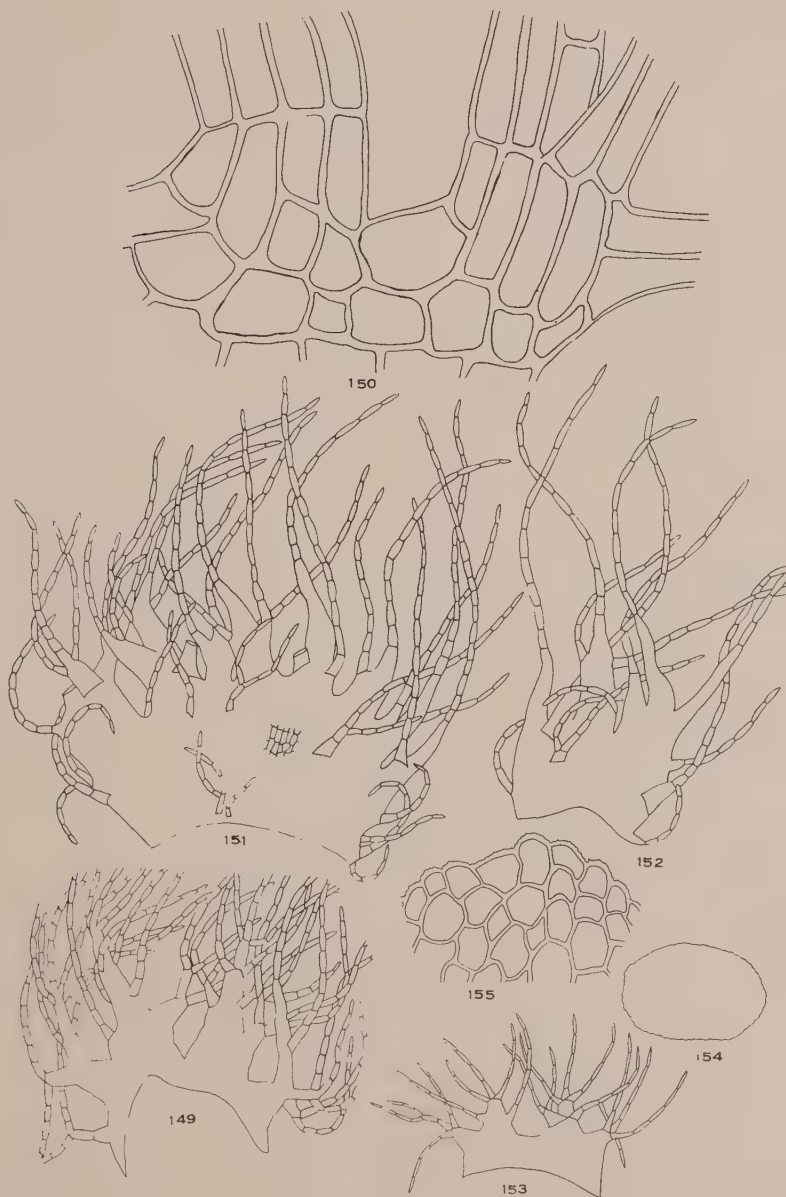
10. TRICHOCOLEA ARGENTEA Herzog, Arch. Bot. Estado S. Paulo 1: 40. 1925.

Plants small, in tufts or scattered among other bryophytes, pale, yellowish-green: stems with leaves to 0.7 mm. wide, 2-3 cm. long, regularly pinnate; stems in cross-section, oval to orbicular, to 9 cells in diameter; cells of the medulla averaging 27  $\mu$ , those of the cortex in a single layer, averaging 19  $\mu$ , cuticle thickened, striolate-papillose; branches mostly 3-4 mm. long; rhizoids not seen: leaves imbricated, subsymmetrical, to 0.6 mm. long, 0.5 mm. wide, divided to one half into 4-5 rarely branched segments; the segment narrowly triangular in outline, sparingly ciliate with opposite, simple, curving cilia; the lamina 4-5 cells long, bearing scattered superficial cilia on the ventral surface; cells of the lamina averaging 38  $\mu$  long, 25  $\mu$  wide, those of the cilia averaging 101  $\mu$  long, 10  $\mu$  wide, the terminal cell often twice the length of the others; the cuticle striolate-papillose: underleaves smaller, to 0.4 mm. long, 0.3 mm. wide, symmetrical, divided to one half into usually 4-5 segments, ciliate as in the leaves: branch leaves and underleaves similar to those of the stem but smaller, with fewer segments, and without superficial cilia on the lamina: male inflorescence subterminal on a stem or branch, the bracts and bracteoles in 9 or more series, similar to the leaves and underleaves but larger, bracts to 0.6 mm.

EXPLANATION OF FIGURES 149-155

FIGS. 149-155. *Trichocolea tomentosa* (Sw.) Gottsche. 149. Stem underleaf,  $\times 55$ . 150. Portion of a stem leaf near the dorsal insertion,  $\times 235$ . 151. Female bract of the innermost series,  $\times 55$ . 152. Innermost female bracteole,  $\times 55$ . 153. Stem underleaf,  $\times 55$ . 154. Cross-section of a stem,  $\times 55$ . 155. Portion of a stem cross-section,  $\times 235$ . FIGS. 149-152, drawn from a portion of the original material of *L. sphagnoides* Spruce (NY); FIGS. 153-155, from a portion of the original material of *T. mexicana* Steph. from Mexico (G).





long, 0.7 mm. wide; bracteoles to 0.4 mm. long, 0.4 mm. wide; antheridia large, globose, borne singly; female inflorescence terminal on a main stem or branch, bracts and bracteoles in three series, the innermost series the largest; bracts subsymmetrical, to 1.3 mm. long, 1 mm. wide, divided to one half into 5-6 often divided segments, ciliate as in the leaves, the lamina 8-9 cells long, bearing numerous scattered superficial cilia; bracteoles symmetrical, to 1.3 mm. long, 0.7 mm. wide, divided into 5-6 unequal, often divided segments, the lamina 8-9 cells long, ciliate as in the bracts; mature sporophyte not seen. (Figs. 118-129).

Habitat: Among other bryophytes.

The distinguishing characteristics of this species include its small size, the regularly pinnate branching habit, the small leaves with usually 4 sparingly ciliate segments, and a lamina bearing scattered superficial cilia.

Distribution: Brazil: Sao Paulo, Estacao Biologico do Alto da Serra, Herzog, no. 7769 (348), the type, (Hb. Herzog).

The species might possibly be confused with *T. flaccida* because of the size and habit, but the two may be separated by the leaves which, in *T. argentea*, bear scattered, superficial cilia on the lamina.

11. TRICHOCOLEA ULEANA Steph., Spec. Hepat. 4: 55. 1909.

Plants medium, in tufts, pale, yellowish-green: stems with leaves to 1 mm. wide, 5 cm. long, pinnate to irregularly bipinnate; stem in cross-section, oval to orbicular, 10-12 cells in diameter; cells of the medulla averaging  $36\ \mu$ , those of the cortex in a single layer, averaging  $23\ \mu$ , cuticle thickened, striolate-papillose; paraphyllia absent; branches mostly 3-4 mm. long; rhizoids not seen: leaves imbricated, asymmetrical, with a very long dorsal insertion, to 0.8 mm. long, 1.3 mm. wide, divided nearly to the base into 5-6 unequal, sometimes branched segments; segment triangular in outline, with a few long, usually simple cilia; the lamina 2-4 cells long, cells subquadrate to rectangular in outline, averaging  $48\ \mu$  long,  $29\ \mu$  wide; cells of the cilia averaging  $92\ \mu$  long,  $13\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, to 0.6 mm. long, 1.1 mm. wide, divided nearly to the base into usually 4 segments, ciliate as in the leaves: branch leaves and underleaves similar to the leaves, but smaller: male and female inflorescence and sporophyte not seen. (Figs. 130-138).

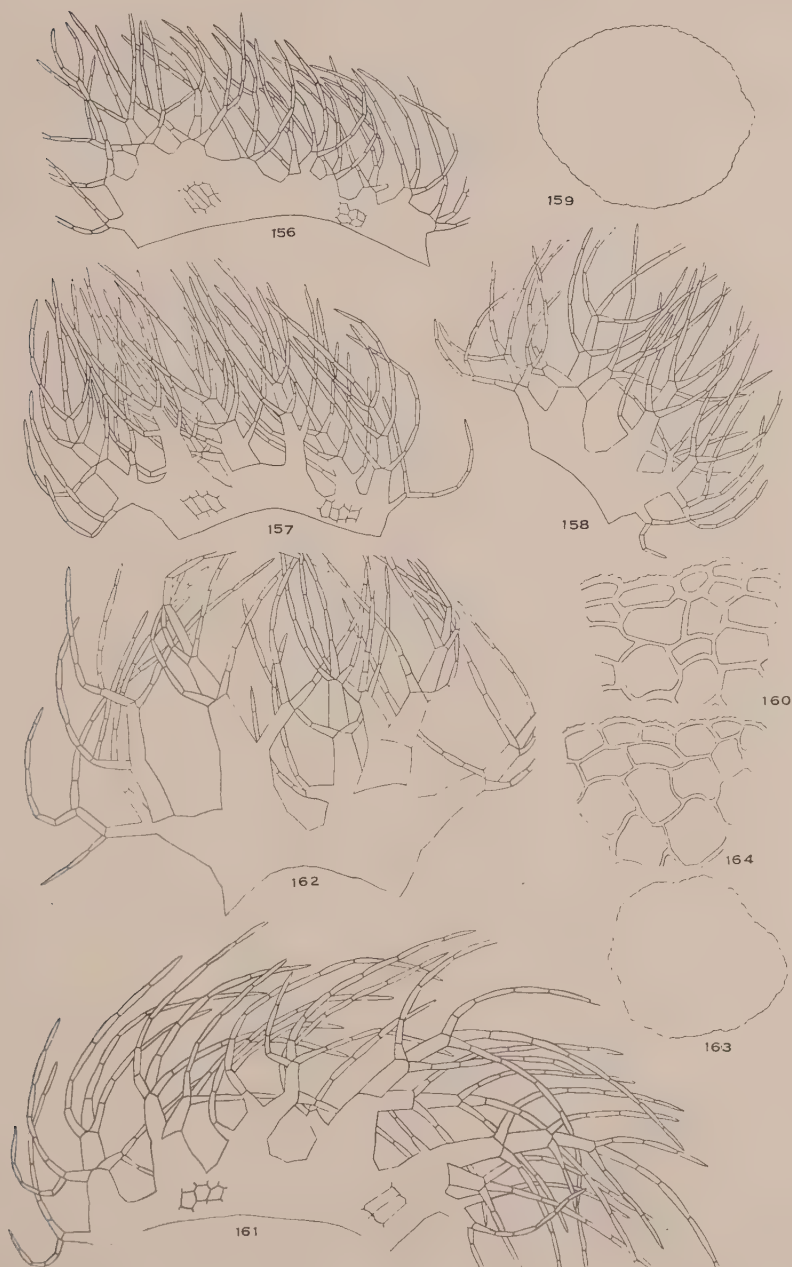
Habitat: On bark.

The distinguishing characters of this species include its medium

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EXPLANATION OF FIGURES 156-164

FIGS. 156-164. *Trichocolea tomentosa* (Sw.) Gottsche. 156. Stem leaf,  $\times 55$ . 157. Stem leaf,  $\times 55$ . 158. Stem underleaf,  $\times 55$ . 159. Cross-section of a stem,  $\times 55$ . 160. Portion of a stem cross-section,  $\times 235$ . 161. Stem leaf,  $\times 55$ . 162. Stem underleaf,  $\times 55$ . 163. Cross-section of a stem,  $\times 55$ . 164. Portion of a stem cross-section,  $\times 235$ . FIG. 156, drawn from a portion of the original material of *T. mexicana* Steph. (G); FIGS. 157-160, from a portion of the original material of *T. Allionii* Steph. from Ecuador (G); FIGS. 161-164, from a portion of the original material of *T. grandifolia* Steph. from British Guiana (G; FH).





size, its leaves with a very long dorsal insertion, a lamina 3–4 cells long, and 5–6 sparsely ciliate segments.

Distribution: Puerto Rico: Sierra de Naguabo, Britton & Hess, (NY).—Brazil: without locality, Ule, no. 202, the original material, (G); Parana, Dusén, no. 2946, (G); Apiahy, Puiggari, no. 257, (G); Sao Paulo, Herzog, no. 7807(250), cited by Herzog (1925, 40).

The species is similar in appearance to both *T. tomentosa* and *T. tomentella* and the distinguishing characteristics are discussed under those species.

12. *TRICHOCOLEA TOMENTOSA* (Sw.) Gottsche, Ann. Sci. Nat. p. 132. 1864.

*Jungermannia tomentosa* Swartz, Prodrumus, p. 145. 1788.

*Basichiton tomentosum* Trev., R. Ist. Lombardo Mem. Sci. Math. Nat. **13**: 394. 1877.

*Leiomitra sphagnoides* Spruce, Trans. & Proc. Bot. Soc. [Edinburgh] **15**: 350. 1885.

*Trichocolea sphagnoides* Steph., Trans. Linn. Soc. Bot. **6**: 99. 1901–05.

*Leiomitra crista-castrensis* Spruce ms., Hepat. Spruc.

*Trichocolea cristacastrensis* Steph., Spec. Hepat. **4**: 59. 1909.

*Trichocolea mexicana* Steph., op. cit. p. 54.

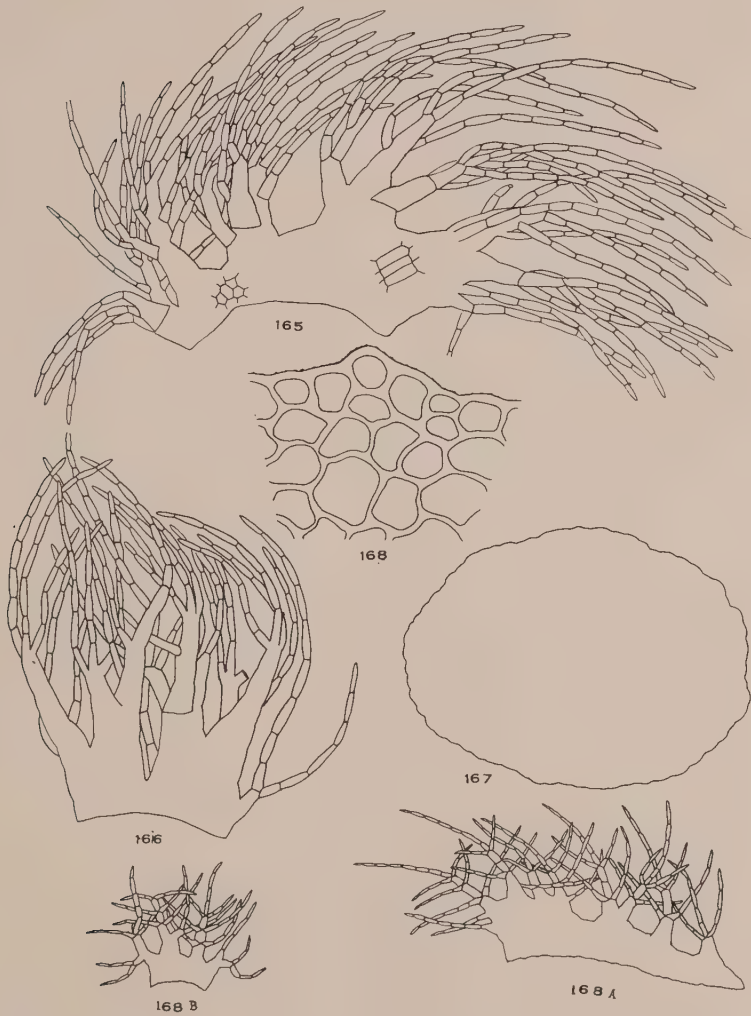
*Trichocolea grandifolia* Steph., op. cit. p. 55.

*Trichocolea Allionii* Steph., Spec. Hepat. **6**: 372. 1924.

*Trichocolea pterophylla* Herzog, Hedwigia **67**: 250. 1927.

Plants robust, in tufts or mats, pale, yellowish-green: stems with leaves to 1.5 mm. wide, 10–20 cm. long, regularly pinnate, occasionally bipinnate; stems in cross-section, oval to orbicular, 21–26 cells in diameter; cells of the medulla averaging  $32\ \mu$ , those of the cortex in 1–2 layers, averaging  $19\ \mu$ , cuticle thickened, striolate-papillose; branches mostly 1 cm. long, becoming recurved in the upper part; rhizoids not seen: leaves closely imbricated, strongly asymmetrical, with a short dorsal insertion, to 1 mm. long, 1.4 mm. wide, divided into 5–8 unequal, often divided segments; the segment triangular in outline, densely long ciliate with simple or branched cilia, segments and cilia strongly curved and closely appressed to the stem; lamina strongly asymmetrical, 1–3 cells long, cells of the dorsal half little longer than broad, averaging  $31\ \mu$  long,  $25\ \mu$  wide, those of the ventral half mostly long rectangular in outline, averaging  $73\ \mu$  long,  $12\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, to 1 mm. long, 0.7 mm. wide, bifid nearly to the base and divided into usually 4 branched segments, cilia similar to those of the leaf: male inflorescence intercalary on a branch, bracts and bracteoles in 6 or more series, similar to the leaves but slightly concave and with a broader lamina; antheridia large, globose, borne singly: female inflorescence terminal on a main stem or branch, bracts and bracteoles symmetrical, bracts to 2 mm. long, 1.7 mm. wide, divided to about half into 6–8 often divided segments, ciliate as in the leaves and with scattered superficial cilia on the lamina; lamina to 16 cells long, cells averaging  $42\ \mu$  long,  $24\ \mu$  wide; bracteoles to 1.3 mm. long, 0.6 mm. wide, deeply divided into usually 4 segments, ciliate as in the bracts, lamina to 8 cells long, with occasional superficial cilia: sporophyte not seen. (Figs. 139–168).

Habitat: On tree trunks and on the ground.



FIGS. 165-168. *Trichocolea tomentosa* (Sw.) Gottsche. 165. Stem leaf,  $\times 55$ . 166. Stem underleaf,  $\times 55$ . 167. Cross-section of a stem,  $\times 55$ . 168. Portion of a stem cross-section,  $\times 235$ . 168A. Stem leaf,  $\times 55$ . 168B. Stem underleaf,  $\times 55$ . FIGS. 165-168, drawn from a portion of the original material of *L. crista-castrensis* Spruce from Ecuador (NY); FIGS. 168A and 168B, from a portion of the original material of *T. pterophylla* Herzog from Brazil (Hb. Herzog).

The distinguishing characteristics of this species include its robust habit, its recurved branches, and its little or not at all decurrent leaves deeply divided into 5–8 long, densely ciliate, curved segments.

Distribution: Jamaica: without locality, Swartz, the original material, (S-PA); Morces Gap, Patterson, (F).—Dominica: Morne Micotrin, Elliott, no. 218, cited by Spruce (1893, 353).—Trinidad: Maraccas Mts., Crüger, (NY).—Mexico: Cafétal, Karsten, the original material of *T. mexicana*, (G); on the lower slopes of El Cerro de Cuguatpetl, Tehuacan, Santos, no. 3640, (F).—Guatemala: Atla Verapaz near Cobán, Türkheim, no. 5810, as *T. mexicana*, (G).—Costa Rica: near La Palma, Maxon, (NY); same locality, Standley, no. 37.565, 38.728; Volcan de Turrialba, Standley, no. 35.155, cited by Herzog (1938, 30); without locality, Brevis, no. 19136, (F).—Colombia: Bogotá, Weir, (NY).—British Guiana: Mt. Roraima, Ule, no. 624, as *T. Allionii*, (G); without locality, Quelch, the original material of *T. grandifolia*, (G; FH). Ecuador: Rosario, Allioni, no. 6643, the original material of *T. Allionii*, (G); Mt. Tunguragua, Spruce, *Hepat. Spruc.*, the original material of *L. crista-castrensis*, (NY); same locality, Spruce, *Hepat. Spruc.*, the original material of *L. sphagnoides*, (NY); Canelos, Spruce, *Hepat. Spruc.*, as *L. tomentosa* var. *canelensis*, p.p. (NY).—Bolivia: without locality, Herzog, no. 4553, as *T. Allionii*, (G); Sillar, Herzog, no. 2736; Comarapa, Herzog, no. 3789; Tabla, Herzog, no. 2798, 4553; Rio Tocarani, Herzog, no. 4037, cited by Herzog (1916, 230) as *T. Allionii*.—Brazil: Alto de Serra, Hoehne, no. 535, (Hb. Herzog), the type of *T. pterophylla*.

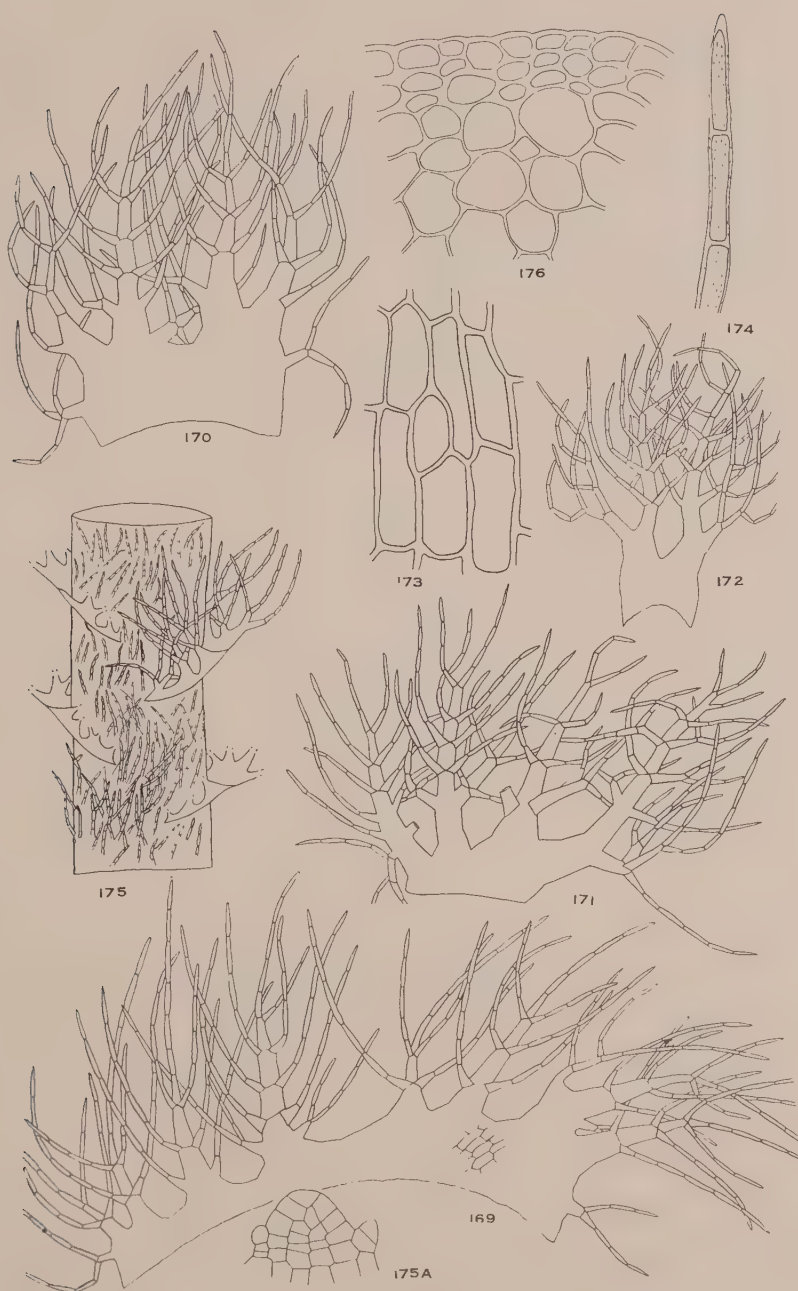
The species is widespread throughout the West Indies and Tropical South America and extends northward through Central America into Mexico. Because of its large size and abundance, it is collected more frequently than most of the other tropical American species of this genus. As in several of the other species, *T. tomentosa* shows a wide range of variation, particularly in the size and configuration of the leaves and underleaves. This wide range of variation due to habitat modifications and/or minor genetic differences, has led to the naming of several very similar species which, in the light of our present knowledge, or more correctly, our lack of knowledge concerning the nature of these variations, should be considered as members of the single, highly variable species, namely, *T. tomentosa*.

*T. sphagnoides* collected in Ecuador, differs from *T. tomentosa* only in having larger leaves and underleaves with longer segments and cilia. (Compare Figs. 139 and 148). *T. grandifolia* collected in Guiana and *L. crista-castrensis* collected in Ecuador, also differ only in size of leaves

#### EXPLANATION OF FIGURES 169–176

FIGS. 169–176. *Trichocolea tomentella* (Ehrh.) Dumort. 169. Stem leaf, ×55. 170. Stem underleaf, ×55. 171. Branch leaf, ×55. 172. Branch underleaf, ×55. 173. Cells from the lamina of a leaf, ×235. 174. Portion of a cilium, ×235. 175. Portion of a stem showing leaf insertion and paraphyllia, dorsal view, ×10. 175A. Median longitudinal section through a stem tip. 176. Portion of a stem cross-section, ×235. FIGS. 169–176, drawn from material collected in Reese's Bog, Cheboygan Co., Michigan by R. Hatcher; FIG. 175A, after Hofmeister (1851).





and underleaves and length of segments and cilia. The lamina of the leaf of *L. crista-castrensis* is more narrow than that of the original material of *T. tomentosa*. (Compare Fig. 139 with Figs. 161 and 165).

The leaves of the original material of *T. mexicana* collected in Southern Mexico, are more sparsely ciliate than those of *T. tomentosa*. (Compare Figs. 139 and 156). In the original material of *T. Allionii* collected in Ecuador, the branching is more irregular than that of *T. tomentosa* and the leaves are divided into fewer segments, but aside from these differences the two are very similar. (Compare Figs. 139 and 157). *T. pterophylla* collected in Brazil, is a very small plant, but its branching habit and the structure of its leaves and underleaves fall within the range of variation of *T. tomentosa* and it is here reduced to synonymy.

The species is similar in general appearance to both *T. Uleana* and *T. tomentella*, but its short dorsal line of leaf insertion separates it from *T. Uleana* while the absence of paraphyllia on its stems separates it from *T. tomentella*.

13. TRICHOCOLEA TOMETELLA (Ehrh.) Dumort., corr. Nees, Naturg. Eur. Leberm. 3: 105. 1838.

*Jungermannia tomentella* Ehrhart, Beiträge zur Naturkunde, 2: 150. 1788.

*Trichocolea tomentella* Dumort., Comment. Bot. 113. 1822.

*Thricocolea tomentella* Dumort., Syllog. Jungerm. 67. 1831.

*Tricocolea tomentella* Dumort., op. cit. p. 99.

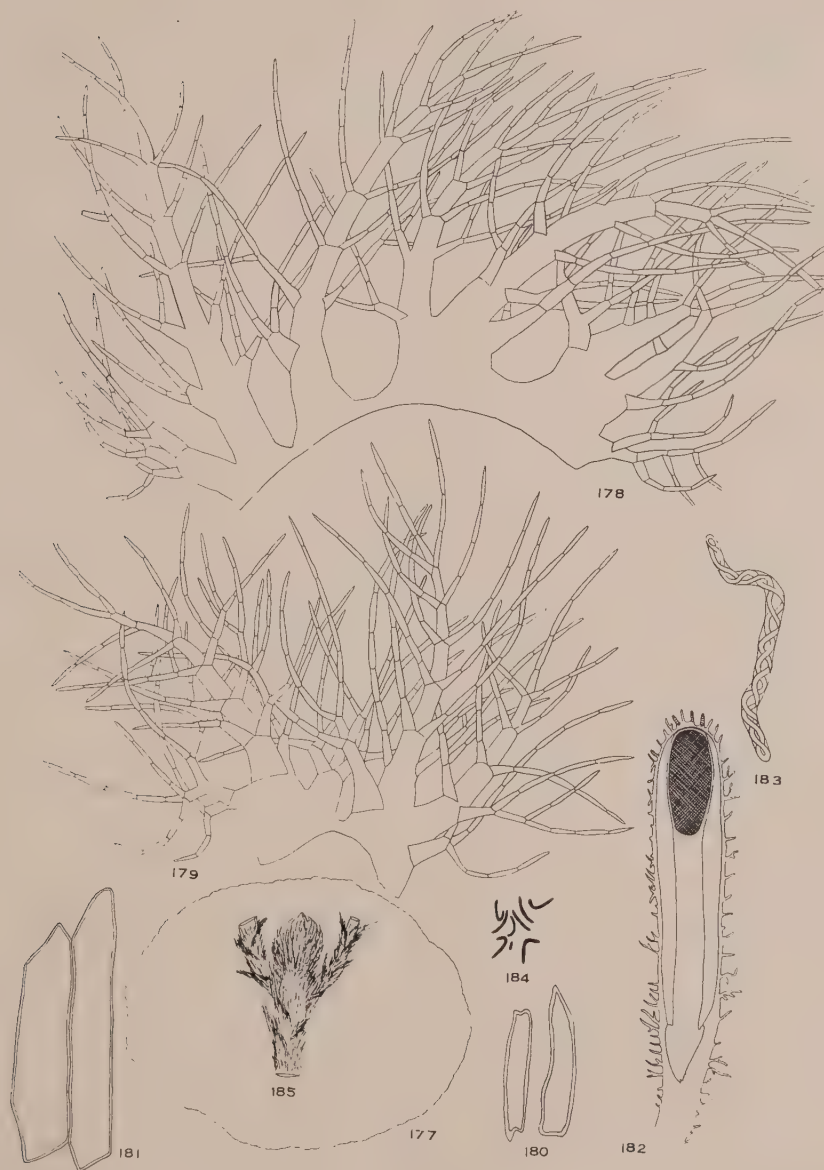
*Trichocolea tomentella* Dumort., Rec. d'Observ. Jungerm. 20. 1835.

*Trichocolea Biddlecomiae* Austin, Bot. Gaz. 3: 6. 1878.

Plants robust, in tufts or mats, pale, whitish-green to yellowish-green: stems with leaves to 2 mm. wide, 5–10 cm. long, regularly bipinnate; stem in cross-section, oval to orbicular, 25–35 cells in diameter; cells of the medulla averaging 42  $\mu$ , those of the cortex in 3–5 layers, averaging 19  $\mu$ ; cuticle thickened, striolate-papillose; paraphyllia abundant except on the ventral side, uniseriate, 5–8 cells long, occasionally branched; primary branches mostly 1 cm. long; rhizoids not seen: leaves distant to imbricated, asymmetrical, to 1 mm. long, 2 mm. wide, divided nearly to the base into 6–8 unequal, often divided segments; the segment triangular in outline, densely ciliate with long, simple or branched, usually opposite cilia, the segments and cilia curved and closely appressed to the stem; lamina to 3 cells long, the cells mostly rectangular in outline, averaging 62  $\mu$  long, 28  $\mu$  wide; cells

#### EXPLANATION OF FIGURES 177–185

FIGS. 177–185. *Trichocolea tomentella* (Ehrh.) Dumort. 177. Cross-section of a stem,  $\times 55$ . 178. Female bract of the innermost series,  $\times 55$ . 179. Innermost female bracteole,  $\times 55$ . 180. Cortical cells from a stem,  $\times 235$ . 181. Medullary cells from a stem,  $\times 235$ . 182. Median longitudinal section through a sporophyte,  $\times 9$ . 183. Elater,  $\times 235$ . 184. Chromosomes from a stem-tip smear preparation,  $\times 3600$ . 185. Stem tip showing position of female inflorescence and subfloral innovations,  $\times 5$ . FIGS. 177–181, 183, and 185, drawn from material collected in Reese's Bog, Cheboygan Co., Michigan by R. Hatcher; FIG. 184, from material collected in Jackson Co., Illinois by R. Hatcher (Sm); FIG. 182, after K. Müller in *Rabenhorst's Kryptogamen-Flora* (1912–16).





of the cilia averaging  $63\ \mu$  long,  $19\ \mu$  wide; the cuticle striolate-papillose: underleaves smaller, to 1 mm. long, 1 mm. wide, bifid and deeply divided into usually 4 often divided segments, cilia similar to those of the leaf: branch leaves and underleaves similar to those of the stem but smaller and with fewer segments: female inflorescence terminal on a main stem or branch, bracts and bracteoles in three series, the innermost series the largest; bracts similar to the leaves but larger, to 1.2 mm. long, 2 mm. wide, divided nearly to the base into 6-7 unequal, often divided segments; bracteoles to 1.2 mm. long, 1.3 mm. wide, deeply divided into usually 4 segments: sporophyte enclosed in a club-shaped coelocaulis; sporangium large, oblong; elaters  $117\ \mu$  long,  $10\ \mu$  wide, reddish-brown, with 2 spirals and with rounded or tapering ends; spores not seen. (Figs. 169-185).

Habitat: On the ground in bogs and on moist, shaded rocks in woods.

The distinguishing characteristics of this species include its large size, the regular branching habit, which is bipinnate to sometimes tripinnate, and the abundant paraphyllia on the stem.

This is a circumpolar species of the Northern Hemisphere which, on the North American Continent, has been reported from Newfoundland in the north, southward along the east coast of the United States to Florida, and westward into Wisconsin and Missouri.

Distribution: Newfoundland: Bay of Islands, Howe & Lang, no. 1172, (FH) and (NY).—Nova Scotia: Windsor Junction, Howe & Lang, no. 440, (NY); Cape Breton Island, Nichols, (NY).—Quebec: Carleton, Collins, Fernald, & Pease, no. 3373, (FH); Grand Coupe, Perce, Collins, Fernald, & Pease, no. 3740a, (FH).—Ontario: Ottawa Macoun, no. 150, (FH).—Maine: Denmark, Bailey, no. 17, (NY); Mount Desert Island, Rand, (NY); Aroostock Co., Fernald, no. 637, (FH); Monmouth, Merrill, (NY).—New Hampshire: Crawford, Faxon, (FH); Mt. Willard, Faxon, (FH); White Mountains, James, (FH); Franconia Mts., Evans, Haynes, et al., (NY); Shelburne, Farlow, (FH); Colebrook, Evans, (FH).—Vermont: Willoughby, Faxon, (FH); Sutton, Faxon, (FH); Leicester, Dutton, no. 1063, (FH); Monkton, Correll, no. 7793, (FH).—Massachusetts: South Hingham, Seymour, (FH); Granville, Seymour, (NY); Tyngham, Berkshire Co., Vail, (NY).—Connecticut: New Haven, Setchell, (NY).—Rhode Island: North Smithfield, Collins, no. 1844, (FH).—New York: Onondaga, Underwood & Cook, (NY); Yonkers, Howe, (NY); Newark Valley, Barbour, (NY); Tannersville, Vail, (NY); Jamesville, Howe, (NY); Chilson Lake, Britton, (NY); near Lake Placid, Britton, (NY); Ithaca, Coville, (NY); Oneida, Maxon, no. 4566, (FH).—Pennsylvania: Wissahickon, James, (NY); Pike Co., James, (FH); Chester Co., James, (FH).—New Jersey: Coytesville, Howe, (NY); Metuchen, Marshall, (FH); Highlands, Haynes, no. 9, (NY).—Delaware: Laurel Commons, (NY).—Maryland: Cockeysville, Plitt, (FH); Camden, Crockett, (FH).—West Virginia: Spruce, Ammons, no. 254, (FH).—District of Columbia: Mt. Pleasant, Washington, Waite, no. H14, (FH).—Virginia: Bull Run Mts., Prince William Co., Allard, no. 4412, (NY); Pine Mountain, Vail & Britton, (NY); Giles Co., Blomquist, no. 3401, (FH); Fulford, (F).—North Carolina: Yancey Co., Atkinson,

no. 11769, (FH); Highlands, Welch, no. 2607, (FH); Soco Falls, Maggie Co., Blomquist, (SM); Greensboro, Schallert, no. 1200, (SM).—South Carolina: Pickens Co., Correll, no. 11002, (FH).—Georgia: Ringgold, Small, no. 5087, (NY).—Florida: Gadsden Co., Kurz, no. 301, (SM).—Tennessee: South Pittsburg, Pollard & Maxon, no. 405, (NY); Chimney's Trail, Sevier Co., Sharp, no. 341033, (FH); Roaring Springs, Knox Co., Sharp, no. 357, (FH); between Wartburg and Harriman, Morgan Co., Sharp, no. 34109, (FH); below Elkmont, Sevier Co., Sharp, no. 4010, (FH); Great Smokey Mountains, Sharp, (F).—Kentucky: Harlan Co., Fulford, no. 856, (F); Pine Ridge, Wolfe Co., Fulford, (F); Cumberland National Forest, Menifee Co., Braun, (F); Lewis Co., Fulford, no. 646, (F); McCreary Co., Braun, no. 2011, (F); Pine Mountain, Whitley Co., Braun, no. 2010, (F); Natural Bridge State Park, Fulford, no. 422, (F); Lee Co., Braun, (F); Carter Co., Fulford, no. 826, (F); Letcher Co., Braun, no. 855, (F).—Ohio: Champaign Co., Spence, no. 1878, (FH); same locality, Werner, (NY).—Indiana: Turkey Run State Park, Parke Co., Welch, no. 6316, (NY); Fern, Underwood, (NY).—Illinois: Hickory Ridge, Jackson Co., R. Hatcher, (SM); Oregon, Waite, (NY); Fountain Bluff, Jackson Co., Demetrio, (SM).—Missouri: Montier, Bush, no. 5313, (NY); east of Picke, Steyermark, no. 10, (FH).—Wisconsin: Bailey's Harbor, Door Co., Curtis, (SM); without locality, Underwood, (NY).—Michigan: Ann Arbor, Pieters, (NY); near Burt Lake, Cheboygan Co., Nichols, no. 537, (NY); Ontonagon Mts., Nichols & Steere, (SM); Sugar Island, Chippewa Co., Steere, no. 3293, (FH); Cecil Bay, Emmet Co., Wynne, no. 2664, (NY); Reese's Bog, Cheboygan Co., Wynne, no. 1187, (NY); Bois Blanc Island, Mackinac Co., Wynne, no. 2588, (NY).

*Jungermannia tomentella*, the type species of the genus *Trichocolea*, is the only species thus far recorded in North America north of Mexico and it is widely distributed in the Northern Hemisphere. In North America, it is found from Newfoundland south to Florida along the east coast and westward into Tennessee, Kentucky, Iowa, Missouri, and Wisconsin.

Within this geographic range, variations in the size of the plants, their growth habit, and the size and number of divisions of the leaves are to be found. In the northern United States where the species reaches its maximum development, the plants become suberect with large, regularly bipinnate to tripinnate stems with leaves divided into 6–8 long, ciliate segments. In the southeastern states and in the midwest, the plants grow prostrate upon the substratum and are generally smaller in size. Where moisture is abundant and more or less continuous throughout the year, the plants are slender and rather distantly pinnate or occasionally irregularly bipinnate. Under drier conditions, the plants show a more compact growth habit with short, closely bipinnate stems and smaller leaves with only 4–6 segments.

Austin (1878) described a species, *T. Biddlecomiae*, found growing on a decaying log in a cedar swamp near Urbana, Ohio, in 1867. In his very brief description of the latter, Austin said that the plants were much smaller than the smallest form of *T. tomentella* that he had ever observed and could be readily distinguished by their simply and rather

distantly pinnate stems. Underwood (1889) suggested that Austin's species was invalid since it had been imperfectly described and was not represented by herbarium specimens. However, on examining the material of *T. tomentella* in the Herbarium of the New York Botanical Garden, a packet of this material from Urbana, Ohio, bearing the correct date was found and undoubtedly represents the original collection. It is quite different from well-developed, healthy plants of *T. tomentella*, but when it is compared with poorly developed specimens of the latter, grown under adverse ecological conditions, the two are indistinguishable. The plants are quite small (0.7 mm. across) and distantly short pinnate. The leaves are much reduced in size, measuring only 0.4 mm. long and 0.6 mm. wide and are divided nearly to the base into 4 short, sparsely ciliate segments. The underleaves are similar to those of well-developed stems of *T. tomentella*, but are only 0.3 mm. long, and 0.5 mm. wide.

Growth in *Trichocolea tomentella* is by means of a pyramidal apical cell with three cutting faces and leaves and lateral branches are arranged on the stem in a sinistorse spiral. This arrangement, however, is sometimes reversed on subfloral innovations, and the leaves and branches are aligned in a dextorse spiral. Evans (1912) has described four types of terminal branching in the leafy liverworts and of these, the *Frullania Type* is the one found in the formation of lateral branches in *T. tomentella*. In this type of branching the apical cell of the new branch is formed in the ventral half of a leaf initial, and only the dorsal portion of this leaf initial goes into the formation of the leaf which is incomplete. The lateral branch thus formed is of limited growth.

Very soon after cessation of terminal growth of a main stem because of the formation of the archegonia, one to several subfloral innovations or branches arise. They appear to be of the *Radula Type* and arise from a cortical cell adjacent to the base of a complete leaf. They are of unlimited growth and may themselves eventually terminate in female inflorescences with subfloral innovations.

The stem is made up of a central cylinder, the medulla, composed of long, hyaline, thin-walled cells with acute or oblique end walls (Fig. 181) surrounded by a cortical sheath several cell layers in thickness which is composed of smaller and shorter, slightly more thick-walled cells which contain chlorophyll (Fig. 180). It is from the exposed surface of the outer layer of these cortical cells that the long, uniseriate, often branched paraphyllia arise. The walls of cortical cells, leaf cells (Fig. 174), and paraphyllia are thickened and minutely striolate-papillose.

According to Macvicar (1926, 357), the male inflorescence is terminal on a main stem or branch. The bracts are similar to the leaves, but with more connivant segments and the antheridia are large, globose, and borne in pairs.

Fertile plants of this species are rarely collected and many of the early stages in sporophyte development are imperfectly or not at all known. The fact that the plants are dioicous would account for the absence of sporophytes in isolated patches where only male or female plants had developed. However, since the female inflorescence (Fig. 182) is made inconspicuous by the dense development of paraphyllia which covers it, it may be easily overlooked.



According to Knapp (1930, 105-113), K. Müller (1951, 120-122), and others, the young developing sporophyte, following fertilization, penetrates downward into the stem tissue. Simultaneously, the ring of stem tissue surrounding the young sporophyte grows upward and completely encloses the latter. Subsequently, the sporophyte becomes differentiated into an haustorial foot, a seta, and a capsule surrounded by a club-shaped, thick-walled prolongation of the stem tissue (Fig. 182) to which Goebel (1930, 862) applied the term *coelocaule*. A perianth is absent. On the outer surface, the *coelocaule* is obscured by a dense development of paraphyllia. It is surrounded by the bracts and bracteoles of which there are three series, with the innermost series the largest. Numerous sterile archegonia are to be found scattered irregularly about the top of the *coelocaule*. The latter remain recognizable long after the maturation and dehiscence of the sporophyte and may still be found on the old *coelocaule* which had developed the previous year.

Upon maturation of the sporophyte and elongation of the stalk, the tip of the *coelocaule* is ruptured irregularly by the emerging sporangium. The sporangium dehisces by the breaking of its wall into four valves and the spores are released.

According to Leitgeb (1875, 67), spore germination in *Trichocolea* may be similar to that of *Lophocolea* in which the spore, upon germination, produces a short uniseriate filament, the end cell of which ultimately cuts off a pyramidal apical cell. In other cases, however, he found that germination resulted in the development of a globose cell mass before the apical cell was formed. With regard to this, Miss Fulford (1954; 1957) suggests that spores of many species, when germinated in an inadequate growth medium, show the filamentous development mentioned above, even though the spores of these same species characteristically produce a globose cell mass outside the exospore. It may be, therefore, that the normal sporeling pattern in *Trichocolea* is that of the latter or *Nardia Type* in which, on germination of the spore, an irregular, globose, multicellular protonema is formed.

As is the case with the vast majority of the leafy liverworts, very little is known concerning the genetics of *Trichocolea*. Heitz (1928) found nine chromosomes as the haploid number for *T. tomentella* and Tatuno (1941) verified this count in Japanese material. Figure 184 represents the haploid chromosome constitution as seen in a stem-tip smear preparation from material collected in Illinois.

*T. tomentella* may be distinguished from *T. tomentosa* with which it might be confused, by its stem paraphyllia and its regular bi-tripinnate branching. Paraphyllia are absent in *T. tomentosa* and the plants are pinnate to occasionally bipinnate.

#### SPECIES NOT AVAILABLE FOR THIS STUDY

TRICHOCOLEA TOMENTOSA var. PLATYCLADA Spruce, Journ. Linnean Soc. 30: 353. 1895.

#### DISTRIBUTION

Stephani, in the *Species Hepaticarum*, recognized 48 species of *Trichocolea* of which 29 were reported from the Americas. He wrongly

cited the distribution of *T. elegans* Lehmann, a temperate South American species, as Swan River, Australia. Since the completion of Stephani's monograph, three additional species have been described and, of the 33 species studied, 20 are here reduced to synonymy. One variety, *T. tomentosa* var. *platyclada* Spruce was not available for examination.

Only one species, *T. tomentella* is known to occur north of Mexico and it has been reported from as far north as Newfoundland, and along the east coast of North America south into Florida, and west into Iowa, Missouri, and Wisconsin. It is also widely distributed in Europe and Asia. Three species, *T. tomentosa*, *T. flaccida*, and *T. paraphyllina* have been collected in Southern Mexico, tropical South America, and the West Indies. *T. Sprucei* is known only from Ecuador. *T. filicaulis* and *T. brevifissa* have been collected in the West Indies and South America. *T. argentea* and *T. Uleana* are known from Brazil and *T. Uleana* has been found in the West Indies. *T. robusta*, *T. floccosa*, and *T. Elliottii* have been collected in the West Indies and *T. Elliottii* has also been found on Juan Fernandez Island near the west coast of temperate South America. *T. elegans* is known only from temperate South America.

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## Cyprinid Fishes of the Subgenus *Cyprinella* of *Notropis*. II. Distribution and Variation of *Notropis spilopterus*, with the Description of a New Subspecies

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The Spotfin Shiner, *Notropis spilopterus*, is an abundant species through most of the northeastern part of the United States. In the course of a revisionary study of the subgenus *Cyprinella* (Gibbs, 1957) the major patterns of geographic variation in this species have been elucidated and the existence of a hitherto undescribed subspecies recognized. It is the purpose of this paper to redescribe the species, since no truly satisfactory definition has been found, to make known its patterns of geographic variation, including the description of the new subspecies, and to differentiate it from several species with which it has long been confused.

### MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Specimens used in this study were located in the following institutions: Academy of Natural Sciences of Philadelphia (abbreviated ANSP in the text), Cornell University (CU), Museum of Zoology, University of Michigan, and the United States National Museum. Grateful appreciation for placing them at my disposal is due their respective staff members: James Böhlke, Edward C. Raney, Reeve M. Bailey, Leonard P. Schultz, Ernest A. Lachner, and Robert H. Kanazawa.

Seven meristic and nine proportional characters have been analyzed, the significant ones of which are shown in Tables 3-6. These counts and measurements were made as described by Hubbs and Lagler (1947), with the exception of postdorsal length (origin of dorsal fin to caudal base) and the distance from dorsal origin to lateral line.

When an adequate number of samples was available from a river system, the number of collections used for counts and measurements from a single area was limited, and usually no more than ten specimens were counted from any single collection. In this manner a certain amount of geographical bias was eliminated. Proportional measurements were made only on specimens between 50 and 60 mm. standard length. Without using regression analysis, this method allows confidence that changes due to allometric growth are minimized. Although this does not necessarily indicate the situation in fishes smaller or larger than those used, the size range chosen is that of a large proportion of the sampled populations.

This study is part of a thesis presented to the faculty of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author is grateful to Dr. Edward C. Raney for his guidance and criticisms and to Dr. George A. Moore for comments on the manuscript, as well as to many others who gave information, advice, and encouragement.

## NOTROPIS SPILOPTERUS (Cope)

## Spotfin Shiner

*Description*.—Pharyngeal teeth 1, 4-4, 1, hooked, the cutting surfaces narrow, concave, with serrations present or absent. Anal rays 8; pectoral rays usually 13-15. Dorsal fin moderate in size, the second or third principal ray longest, the posterior rays extending beyond the anterior in the depressed fin, the origin nearer caudal base than snout.

Lateral-line scales usually 35-39, variable between subspecies. Predorsal circumferential scales usually 13-2-11, often 15-2-11; caudal peduncle scales 7-2-5. Scales not crowded before dorsal. Lateral scales with their exposed edges higher than wide, especially immediately above and below the lateral line.

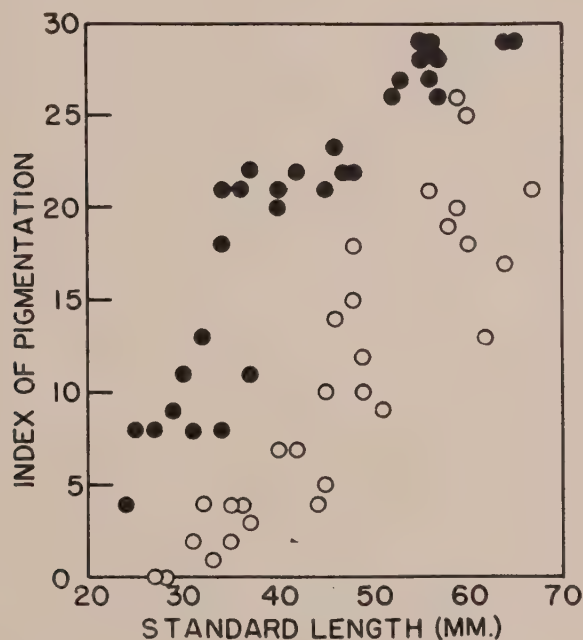


FIG. 1. Graphic representation of dorsal fin pigmentation in *Notropis whipplei* (black dots) and *N. spilopterus* (open dots). See text for explanation.

Head length usually 24-27% of standard length, the snout conical or subconical. Orbit usually 7-8% of standard length, shorter than snout,  $3\frac{1}{2}$ -4 in head. Mouth terminal or subterminal, oblique, moderately large, end of upper jaw reaching about to anterior edge of eye; upper jaw usually slightly longer than lower jaw and slightly longer than orbit.

Body slender to deep, the degree varying between (and to some extent within) subspecies. Lateral line slightly decurved from opercular margin to below middle of dorsal fin.

Nuptial tubercles in breeding males as follows: top of head (Fig.

4, bottom) with scattered tubercles which are larger than elsewhere; snout with dense moderate tubercles, a hiatus between those of snout and top of head. Notal ridge with densely scattered moderate-sized tubercles on nape, becoming smaller and less extensive toward the dorsal origin. Each mandibular ramus with a single row of tubercles, smaller than those of top of head. Body with very small tubercles on dorsal and lateral scale surfaces, tending to be arranged several in an arc along each exposed scale margin; caudal peduncle quite heavily

TABLE 1.—*Tabulation of index of pigmentation of dorsal fin in Notropis s. spilopterus from Wheeling Cr. near Elm Grove, Ohio Co., W. Va.*

Standard Length (mm.)	I	II	Membrane			VI	VII	Total Index
			III	IV	V			
26.5	0	0	0	0	0	0	0	0
28.4	0	0	0	0	0	0	0	0
31.4	0	0	0	0	0	2	0	2
31.6	0	0	0	0	1	2	1	4
33.4	0	0	0	0	0	1	0	1
35.3	0	0	0	0	1	2	1	4
35.3	0	0	0	0	0	2	0	2
35.9	0	0	0	0	1	2	1	4
36.3	0	0	0	0	0	2	1	3
37.2	0	0	0	0	0	2	1	3
40.3	0	0	0	0	2	3	2	7
42.4	0	0	0	0	2	3	2	7
43.5	0	0	0	0	1	2	1	4
44.5	0	0	0	0	2	4	4	10
44.5	0	0	0	0	0	3	2	5
45.6	0	0	1	2	3	4	4	14
48.1	1	1	2	3	3	5	4	19
48.2	0	0	0	0	5	5	5	15
49.2	0	0	0	1	2	4	3	10
49.3	0	0	0	0	4	4	4	12
50.9	0	0	0	0	2	4	3	9
56.4	1	2	2	3	3	5	5	21
58.0	1	1	2	2	3	5	5	19
58.5	3	3	3	3	4	5	5	26
59.2	0	2	2	3	4	5	5	20
59.8	2	3	3	3	4	5	5	26
59.9	1	1	1	2	3	5	5	18
61.7	0	0	0	1	2	5	5	13
64.3	0	0	0	2	5	5	5	17
67.2	1	1	2	3	4	5	5	21

tuberculate, especially in the western subspecies. Belly without tubercles. A row of tubercles on the upper surface of rays of pectoral and pelvic fins, on both sides of anal rays, and less well-developed on dorsal and caudal rays, in each case following branchings of the rays.

*Coloration*.—Scales above lateral line and a few rows below it narrowly edged in black, appearing diamond-shaped in outline. A plumbeous lateral stripe present on posterior half of body. This is often barely discernible, but at the height of its development, in breeding specimens, it is prominent, dark and wide, occupying almost the middle third of the width of the caudal peduncle. Anterior to the



dorsal origin the lateral stripe becomes less dense and somewhat wider, continuing as a diffuse band to the opercular margin. In some specimens with light background coloration, the anterior portion of the stripe is also quite prominent. A dark, narrow humeral bar present behind the opercular margin, reaching from the dorsal part of the opercular opening to the base of the pectoral fin.

Top of head dark plumbeous, the dense color extending to the lower

TABLE 2.—*Tabulation of index of pigmentation of dorsal fin in Notropis whipplei from Elk R., 2.2 mi. W. Fayetteville, Lincoln Co., Tenn. and Caston Cr., SE Okla.*

Standard Length (mm.)	I	II	Membrane			VI	VII	Total Index
			III	IV	V			
23.7	0	0	1	1	1	1	0	4
24.5	0	1	2	2	2	1	0	8
27.0	0	2	2	2	1	1	0	8
29.4	0	1	2	2	2	1	1	9
29.5	0	1	2	2	2	2	2	11
29.8	0	1	2	2	2	2	2	11
30.3	0	1	2	2	2	2	1	10
31.2	0	1	2	2	2	1	1	9
31.4	0	0	2	2	1	2	1	8
32.3	1	2	2	2	2	2	2	13
33.5	1	3	3	3	3	3	2	18
33.6	0	1	1	2	2	2	0	8
34.4	3	3	3	3	3	3	3	21
36.4	3	3	3	3	3	3	3	21
37.2	0	1	1	1	2	3	3	11
37.4	2	3	3	3	4	4	3	22
39.8	1	3	3	3	3	4	3	20
39.9	2	2	3	3	3	4	4	21
42.3	3	3	3	3	3	4	3	22
45.2	2	2	3	3	3	4	4	21
46.1	3	3	3	3	3	4	4	23
46.1	3	3	3	3	3	4	4	23
46.6	2	3	3	3	3	4	4	22
47.5	2	3	3	3	3	4	4	22
52.0	3	3	3	3	4	5	5	26
52.6	3	3	4	4	5	5	3	27
54.6	3	3	4	4	4	5	5	28
55.1	3	4	4	4	4	5	5	29
55.7	2	3	4	4	4	5	5	27
56.3	3	4	4	4	4	5	5	29
56.5	3	3	4	4	4	5	5	28
57.3	3	3	3	3	4	5	5	26
63.9	3	4	4	4	4	5	5	29
64.9	3	4	4	4	4	5	5	29

edge of the eye on the snout, and behind the eye not quite to its dorsal margin. Diffuse melanophores present on side of head behind eye to a level just below the orbit. Rim of upper jaw usually very darkly pigmented, contrasting markedly with the plumbeous snout above, with the light mouth lining immediately below, and with the moderately pigmented lower jaw.

A narrow middorsal stripe present, slightly wider before the dorsal fin than behind, continuing almost undiminished to the base of the

procurent caudal rays. Ventral pigment absent except for a narrow, deep-lying bar between the chin rami.

Dorsal fin lightly pigmented except in breeding males. Very small specimens to about 30 mm. show little or no trace of pigment, even in the last two interradi al membranes. Progressively, but slowly, the rear membranes become more heavily pigmented, but only in breeding males do all the membranes show a noticeable concentration of melanophores. In specimens which lack well-developed tubercles, the first three interradi al membranes (behind principal rays 1-3) seldom

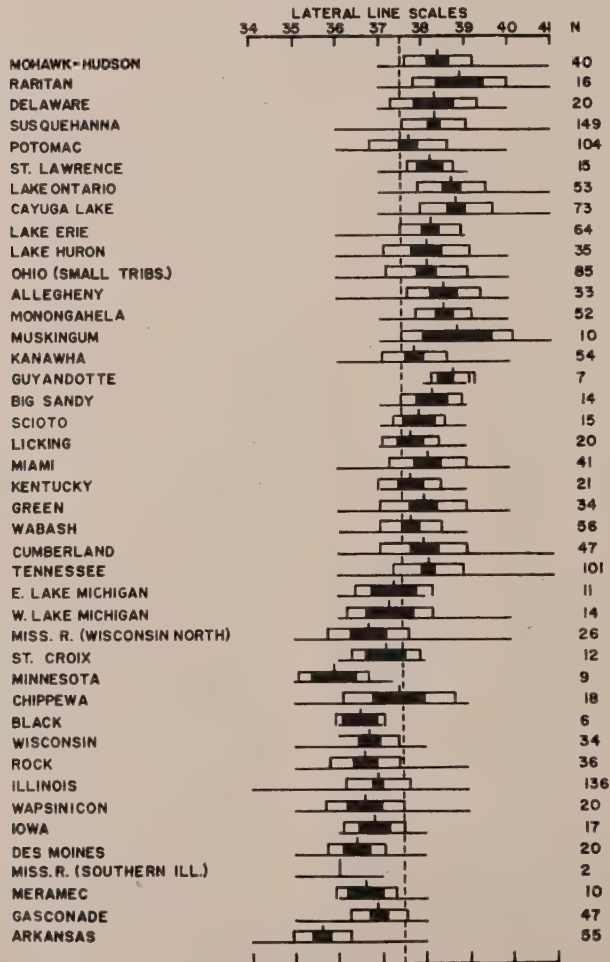


FIG. 2. Graphic analysis of lateral-line scales in *Notropis spilopterus*. Horizontal line=range; vertical line=mean; open rectangle=one standard deviation on each side of mean; black rectangle=twice the standard error on each side of mean. (Hubbs and Hubbs, 1953). The dashed line between 37 and 38 is the line of best separation of the two subspecies.

show any pigment except that which lines the rays. When any is present, there are only a few melanophores. The fourth membrane begins to develop a moderate concentration of pigment in fish around 45 mm. or longer, but seldom becomes dark. The three posterior membranes develop pigmentation somewhat more rapidly. This development of dorsal fin pigment, useful in distinguishing this species from *N. analostanus* and *N. whipplei*, is shown in Tables 1 and 2 and Fig. 1. In the scatter diagram, an arbitrary index of dorsal fin pigmentation has been plotted against standard length. The index was determined by rating the degree of pigmentation on each membrane on a scale of 0 to 5 and taking the sum of these scores for each specimen. A fin which was darkly pigmented on all seven membranes would show an index of 35. The procedure was carried out in two collections of *whipplei* (one collection used for larger specimens which were lacking in the other) and one of *spilopterus*, both groups of which are representative of the respective species, regardless of subspecies, throughout their ranges. Since *analostanus* is similar in dorsal fin pigmentation to *whipplei*, the diagram for the latter represents either species equally well.

Inside of first pectoral ray often lined with black; pelvic and anal fins usually without melanophores. Caudal lightly pigmented, often slightly lighter at base than distally.

In breeding males the overall coloration becomes darker, and occasionally a diffuse, roundish dark patch develops in the mid-lateral region, somewhat similar to that seen in *Notropis venustus*, the Black-tail Shiner. The unpaired fins assume a yellowish coloration, and all the fins become more or less milky.

**Diagnosis.**—A species of the subgenus *Cyprinella*, having lateral scales narrowly outlined in black, appearing diamond-shaped, and the last two interradial membranes of the dorsal fin rather darkly pigmented. Lateral-line scales usually 35–40; predorsal circumferential scales usually 13–2–11, often 15–2–11; caudal peduncle scales 7–2–5. Anal rays 8; pectoral rays usually 13 or 14. Teeth 1, 4–4, 1. No caudal spot or depigmented areas at base of caudal.

Breeding males with unpaired fins yellowish; dorsal not greatly enlarged. Breeding tubercles of nape smaller than those of top of head, *but only slightly so*; a hiatus between tubercles of snout and top of head. Mandibular tubercles smaller than those of top of head.

Comparisons will be made in the subspecific diagnoses.

#### NOTROPIS SPILOPTERUS SPILOPTERUS (Cope) Eastern Spotfin Shiner

*Photogenis spilopterus*—Cope, 1866: 378 (orig. descr.); 1867: 162, 166 (Char.); Jordan and Copeland, 1876: 154 (designated type species of *Photogenis*; Jordan and Gilbert, 1877: 94.

*Leuciscus spilopterus*—Günther, 1868: 256 (specimens from Cope coll.).

*Plargyrus spilopterus*—Jordan, 1876: 289 (char., distr.).

*Minnilus spilopterus*—Jordan, 1877: 45, 80 (Maumee and Tippecanoe Rivers, Ind.).

*Photogenis spiloptera*—Klippart, 1877: 53 (Ohio).

*Notropis whippaii spilopterus*—Hubbs and Greene, 1928: 381 (Great Lakes form distinguished from Arkansas form = true *whipplei*); Greeley, 1929: 171 (Erie system, N.Y.); Hubbs and Brown, 1929: 33 (Ontario); Greeley, 1930: 80 (L. Champlain, N.Y.); Hankinson, 1930: 73 (spawning behavior); Osburn, Wickliff

- and Trautman, 1930: 173 (Ohio); Greeley and Greene, 1931: 88 (St. Lawrence system N.Y.); Sibley and Rimsky-Korsakoff, 1931: 118 (St. Lawrence system, N.Y.); Greeley and Bishop, 1932: 85 (Oswegatchie and Black systems, N.Y.); Shurrager, 1932: 386 (Hocking R., Ohio; habitat); Greeley and Bishop, 1933: 97 (Upper Hudson system, N.Y.); Hankinson, 1933: 568 (Mich. inland lakes); Greeley, 1934: 103 (Raquette system, N.Y.); 1935: 94 (Mohawk-Hudson system, N.Y.); Stewart, 1935: 84 (Lewisburg, Pa.); Greeley, 1936: 83 (Susquehanna system, N.Y.); Hubbs and Cooper, 1936: 12, 28, 40, 61 (nesting, char., range in Mich.); Greeley, 1937: 95 (Lower Hudson system, N.Y.); 1938: 67 (Allegheny and Chemung systems, N.Y.); 1940: 74 (L. Ontario systems, N.Y.).
- Notropis spilopterus*—Welter, 1938: 66 (Licking system, Ky.); Kuhne, 1939: 50, 59 (Tenn.); Raney, 1939: 275 (Ohio system, Pa.); Fowler, 1940: 11 (Ohio and Erie systems, Pa.); Shoup and Peyton, 1940: 111, 113 (Cumberland system, Tenn.); Hubbs and Lagler, 1941: 50, 58 (char., distr. in Great Lakes); Shoup, Peyton and Gentry, 1941: 69 (Obey R., Tenn.); Stone, 1941: 288-290 (comp. char., biology); Hubbs and Lagler, 1942: 78 (distinguished from *whipplei*; partly misleading); Shoemaker, 1942: 270, 282 (Wayne Co., Ind.); Radforth, 1944: 60 (dispersal routes in Ontario); Bailey, 1945: 126 (origin in Miss. basin); Gerking, 1945: 14, 20, 61, 62 (distr. in Indiana; habitat); Dymond, 1947: 17, 21 (char., distr. in Canada); Hubbs and Lagler, 1947: 60, 67 (char., distr. in Great Lakes); Dobie, Meehan and Washburn, 1948: 102 (bait; char., habitat, food); Shockley, 1949: 254 (Wabash system, Ind.); Harlan and Speaker, 1951: 81 (char., plate); Bailey, 1951: 193 (Iowa; char.); Fowler, 1952: 106 (N.J.); Legendre, 1952: xi (Quebec); Speirs, 1953: 9 (cites orig. descr.); Legendre, 1954: 14 (Quebec); Schwartz and Tryon, 1954: 288 (Pymatuning L., Pa.); Bailey, 1956: 332 (Iowa; char.).
- Erogala whipplei spilopterus*—Driver, 1950: 287 (char.).
- Hybopsis fretensis*—Cope, 1866: 382 (orig. descr.); Hubbs, 1926: 45 (considered syn. of *Notropis whipplei whipplei* = *spilopterus*).
- Notropis fretensis*—Fowler, 1918: 20 (char.).
- Leuciscus analostanus* (misidentification)—Günther, 1868: 256 (specimens from Cope coll.).
- Photogenis analostanus* (misidentification)—Jordan and Brayton, 1878: 294 (in part; char.).
- Luxilus analostanus* (misidentifications)—Jordan, 1878a: 294 (in part; char., distr.); 1878b: 410, 421 (in part; syn.); 1879: 110 (in part; syn., distr.).
- Hudsonius analostanus* (misidentifications)—Jordan, 1880: 292 (in part; distr., char.); 1882: 845 (in part; Ohio; syn.); 1884: 292 (in part; char., distr.); 1885: 814 (in part).
- Notropis analostanus* (misidentification)—Trititt, Bean and Fowler, 1929: 41 (char., range).
- Cliola whipplei* (misidentification)—Jordan and Gilbert, 1883: 178 (in part; char., distr., syn.).
- Notropis whipplei* (misidentifications)—Jordan, 1889: 158, 167 (in part presumed; Ohio, Wabash systems, Ohio); Meek, 1889a: 437 (Maumee system, Ohio); 1889b: 307 (in part; Cayuga L., N.Y.); McCormick, 1892: 18 (Lorain Co., Ohio; char., distr.); Hay, 1894: 210 (Indiana); Kirsch, 1895: 329 (Maumee system); Jordan, 1899: 58 (in part; char., distr.); 1910: 58 (in part; char., distr.).
- Notropis whipplei* (misidentifications)—Eigenmann and Beeson, 1894: 49 (Indiana); Jordan and Evermann, 1896a: 256 (in part; syn., distr.); 1896b: 278 (in part; char., syn., distr.); Evermann, 1902: 95 (Great Lakes); Evermann and Goldsborough, 1902: 172 (Clear Cr. of Chautauqua L., N.Y.); Evermann and Kendall, 1902a: 212 (L. Ontario); 1902b: 219, 221, 223 (L. Champlain, N.Y.); 1902c: 233, 236 (St. Lawrence R.); Eigenmann and Beeson, 1905: 129 (Indiana); Fowler, 1907: 110 (Ohio system, Pa.); 1909: 537 (Susquehanna and Erie systems, Pa.); 1910: 282 (in part; variation); Hankinson, 1910: 3 (Charleston, Ill.); Meek and Hildebrand, 1910: 272 (in part; char., syn.); Halkett, 1913: 64 (St. Lawrence R. and Great Lakes, U.S.A. and Canada); Hankinson, 1913: 107 (Charleston, Ill.); Fowler, 1918: 25 (char.); 1919: 60 (Ohio and Erie systems, Pa.); Evermann and Clark, 1920: 355 (L. Maxinkuckee, Ind.; char., habits); Fowler, 1923: 10 (Upper Kanawha system, Va.); Hankinson, 1923: 31 (Ontario system, N.Y.); Pratt, 1923: 80 (in part; char., distr.); Greeley, 1927: 50, 59 (Genesee system, N.Y.); Adams and Hankinson, 1928: 350 (Oneida L., N.Y.); Eaton, 1928: 42 (Keuka and Seneca L., N.Y.); Greeley, 1928: 98, 106



- (Oswego system, N.Y.); Sibley, 1929: 187 (Erie system; food); Carpenter, 1930: 197 (L. Champlain basin; food); Rimsky-Korsakoff, 1930: 89, 95 (L. Champlain; forage fish, food).
- Notropis whipplii whipplii* (misidentification)—Hubbs, 1926: 37 (in part; Great Lakes; char.).
- Cyprinella whipplii* (misidentifications)—Jordan, 1929: 81 (in part; char., distr.); Pratt, 1935: 76 (in part; char., distr.); Schrenkeisen, 1938: 129 (in part; char., distr.).
- Erogala whipplii* (misidentifications)—Jordan, Evermann and Clark, 1930: 129 (in part; distr., syn.); Blatchley, 1938: 48 (Indiana); Driver, 1942: 274 (in part; char., distr.).

*Types.*—The only extant type appears to be a poorly preserved specimen in the Academy of Natural Sciences, ANSP 22901, which has been relabeled as *Notropis whipplii* (Girard). According to Cope, the types were collected in the St. Josephs River in southwestern Michigan. This is an area of intergradation, but the type is retained for the eastern subspecies barring refinement of current nomenclatural procedure. It would seem worthwhile to establish the custom of having a type for the species and separate types for each subspecies in a situation such as this.

*Number of collections examined by river systems.*—Mohawk-Hudson, 17; Raritan, 4; Delaware, 7; Susquehanna, 28; Potomac, 14; St. Lawrence, 11; Lake Ontario, 17; Cayuga Lake, 29; Lake Erie, 63; Lake Huron, 26; Ohio River (smaller tribs.), 22; Allegheny, 6; Monongahela, 9; Muskingum, 3; Kanawha, 37; Guyandot, 1; Big Sandy, 6; Scioto, 7; Licking, 5; Miami, 12; Kentucky, 10; Green, 18; Wabash, 15; Cumberland, 32; Tennessee, 61.

*Comparative diagnosis.*—This subspecies is the one on which most previous comparisons and descriptions have been based. Within its range, there are three species of *Cyprinella* with which it may be confused: *analoostanus*, *whipplei*, and *galacturus*. From all of these it differs in having eight, instead of nine, anal rays, and in having less-developed pigment in the dorsal fin (see species description and Fig. 1). It may be distinguished from *galacturus* by the absence of depigmented "wrist" patches at the base of the caudal fin, by its fewer lateral-line scales (37–39, instead of 39–40), by its fewer pectoral rays (modally 14, often 15, instead of 15 or 16), and by the absence of pigment along the anal base (present in *galacturus*). Breeding males of *spilopterus* lack the enlarged dorsal fin and red fin pigment of *galacturus*, and have a hiatus between the tubercles of the snout and top of head which that species lacks.

The external distinctions between *N. s. spilopterus* and either *analoostanus* or *whipplei* are often subtle, even apparently absent on occasion. Considering breeding males only, *N. s. spilopterus* differs from both other species in having yellow fins, in having larger nape tubercles, which, near the occiput, are only slightly smaller than those on the head and are quite apparent (those of *analoostanus* and *whipplei* are smaller and may be difficult to detect), in having the mandibular tubercles smaller than those on top of the head (they are about the same size as the head tubercles in the others), and in lacking melanophores on the anal fin membranes.

It differs further from *analoostanus* in its higher lateral-line scale

count (usually 37–39, instead of 36 or less), and in its slender form (body depth usually 22–25% of standard length, instead of 24–27%).

Its similarity to *whipplei* is striking. The lateral-line scale count is modally the same in both (despite the contrary statement of Hubbs and Lagler, 1942), although *whipplei* does not have as high a range as *N. s. spilopterus*. Body depth overlaps considerably in the two, although tending to be greater in *whipplei*. The only useful character in addition to those already mentioned is the tendency of *whipplei* to have 15 pectoral rays, *spilopterus* 14 or less.

*Range* (Fig. 3).—Tributaries of the Ohio River from the Tennessee and Wabash to the Allegheny; Great Lakes Basin from Lake Huron to

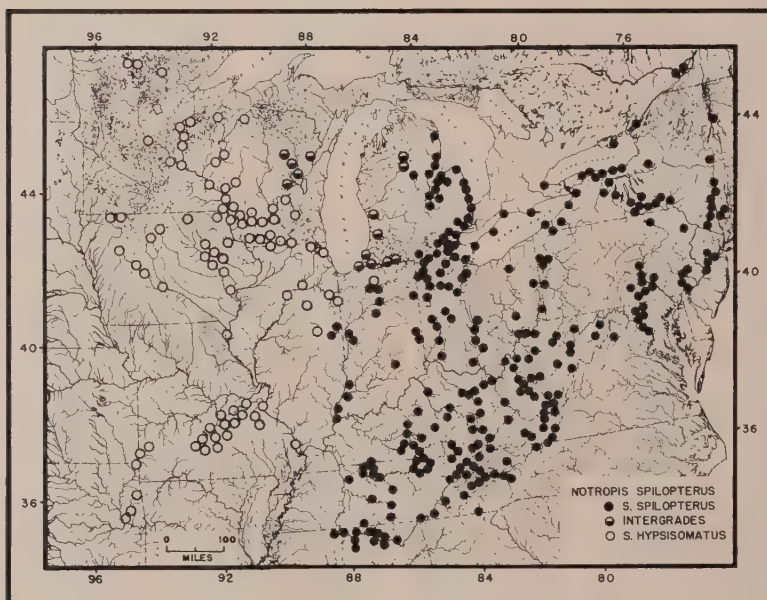


FIG. 3. Distribution map of collections examined.

the St. Lawrence River in Quebec, and Lake Champlain; Atlantic coastal systems from the Mohawk-Hudson southward to the Potomac.

*Habitat*.—Appears to prefer small to moderately large streams, but not extremely small headwater creeks or larger mainstream waters. Found over many types of bottom and in many kinds of water, including larger lakes, but seems to thrive best in running water. Tends commonly to gather in pools along the banks of streams.

*Etymology*.—The specific and subspecific name *spilopterus* is an adjective derived from the Greek *spilos*, spot, and *pteron*, wing or fin, certainly in allusion to the pigment of the last two dorsal interradiar membranes of adults.

**Notropis spilopterus hypsisomatus**, new subspecies

## Western Spotfin Shiner

- Cyprinella galacturus* (misidentification)—Nelson, 1876: 47 (Rock and Illinois systems, Ill.).
- Chiola whipplei* (misidentification)—Jordan and Gilbert, 1883: 178 (in part; char., distr., Syn.).
- Notropis whipplei* (misidentifications)—Forbes, 1884: 77 (Ill.); Jordan and Meek, 1886: 5 (Des Moines system, Iowa); Meek, 1891: 117, 121, 140 (in part; Meramec(?) and Gasconade systems, Mo.); Call, 1892: 50 (Des Moines system, Iowa); Meek, 1892: 221, 223, 226, 228, 233, 239, 240, 242, 244, 246 (Mississippi, Des Moines, Iowa, Wapsinicon, Sioux systems, Iowa); 1893: 109 (Cedar system, Iowa); 1894: 136 (Storm L., Iowa); Surber, 1920: 37 (Upper Mississippi and Minnesota systems, Minn.).
- Notropis whippelii* (misidentifications)—Woolman, 1895: 356, 370 (Minnesota system, Minn.); Cox, 1896: 609 (Minnesota system, Minn.); Evermann and Cox, 1896: 405 (Missouri system); Cox, 1897: 33, 36, 79 (Minn., char.); Forbes, 1909 (Ill. and general distr.); Forbes and Richardson, 1920: 145 (Ill.; char., distr.); Pratt, 1923: 80 (in part; char., distr.); Cahn, 1927: 38 (S. Wisc. distr., habitat); Pott and Jones, 1927: 351 (Iowa records); Hankinson, 1929: 448 (Shenoyenne R., N.D.); Thompson and Hunt, 1930: 24, 37, 38, 40, 43, 53, 56, 81 (Champaign Co., Ill.; char., ecology); O'Donnell, 1935: 482 (Ill. distr., habitat).
- Cyprinella whippelii* (misidentifications)—Jordan, 1929: 81 (in part; char., distr.); Pratt, 1935: 76 (in part; char., distr.); Thompson, 1935: 493 (Ill.; hybridization with *lutrensis* suspected); Schrenkeisen, 1938: 129 (in part; char., distr.).
- Erogala whippelii* (misidentifications)—Hubbs and White, 1923: 104 (Cass L., Minn.); corrected by Hubbs, 1945: 18.
- Notropis whippelii spilopterus*—Friedrich, 1933: 28 (Mississippi R. in Minn.; Greene, 1935: 108 (Wisc.; distr., dispersal routes).
- Erogala whippelii spilopterus*—Driver, 1950: 287 (in part; char., distr.).
- Notropis spilopterus*—Haas, 1943: 163 (Fox and Rock systems, Ill.); Hubbs, 1945 (corrects report of *lutrensis* in Cass L., Minn.); Eddy and Surber, 1947: 159–160; Smith, Johnson and Hiver, 1949: 208 (Root R., Minn.); Moore and Paden, 1950: 85 (Illinois R., Okla.); Starrett, 1950a: 116 (Des Moines system, Iowa); 1950b (food); Bailey, 1951: 193, 221 (Iowa: key); Harlan and Speaker, 1951: 81 (char., plate); Starrett, 1951: 24 (growth); Moore, 1952 (Okla.); Cross, 1954: 475 (Neosho system, Kans.; char., associates); Hall, 1955: 37 (Tenkiller Res., Okla.); Bailey, 1956: 332 (Iowa: key).

*Types*.—Holotype CU 28541, an adult male 68.8 mm. standard length, in breeding condition, collected at Wonder Lake—Bay in north end, McHenry Co., Illinois on July 2, 1950 by James N. Layne and Lois V. Linderorth (now Mrs. Layne). Two paratypes, CU 22305, were both taken with the holotype. The following paratypes were all collected in the Illinois River system, Illinois: *Lake Co.*: CU 17931 (48), DesPlaines R. S of bridge on Ill. 22. *McHenry Co.*: CU 17960 (31), Nippersink Cr. ca. 300 yards N of bridge at Barnards Mill on Wonder Lake Road. CU 17984 (6), Nippersink Cr. at Greenwood on US 14. CU 22326 (12), Wonder L.—Bay at N end. CU 22330 (33), Nippersink Cr. inlet to Wonder L. at Adams Dam. CU 17946 (15), Nippersink Cr. N of dam at Wonder L.

*Number of additional collections examined from each river system, but not designated as paratypes*.—Mississippi River and small tribs from Wisconsin north, 23; St. Croix, 9; Minnesota, 2; Chippewa, 3; Black, 6; Wisconsin, 12; Rock, 12; Illinois, 13; Wapsinicon, 3; Iowa, 8; Des Moines, 8; Mississippi River and small tribs. in S. Illinois and N. Missouri, 4; Meramec, 12; Gasconade, 18; Arkansas (Spring R.), 7; Arkansas (Illinois R.), 7; Missouri (Okoboji, Spirit and Silver Lakes, Iowa), 3.



*Comparative diagnosis.*—This is a deep-bodied form, often closely approaching *Notropis lutrensis* in general configuration. The scales are large, and in breeding males there is a strong tendency to have the area above the anal fin on the lower half of the caudal peduncle heavily tuberculate. In both of these characteristics it also approaches *lutrensis*. Perhaps the reports of intergrades or hybrids between "*whipplei*" and *lutrensis* (Forbes and Richardson, 1920; Thompson, 1935) were based on extreme development of the *lutrensis*-like characters of *N. s. hypsisomatus*.

*Notropis spilopterus hypsisomatus* is compared with the eastern subspecies, *N. s. spilopterus*, in Tables 3–6 and in Fig. 2. It differs chiefly in having usually 36 or 37 lateral-line scales, instead of 37 to 39; in its deeper body, modally 26% of standard length, rather than 24%; and in the greater development of tubercles on the lower part of the caudal peduncle in the breeding male. There are tendencies toward differentiation in other characters, but most of these overlap too greatly to be of use in a diagnosis.

The distinction between these two subspecies is more consistent than appears at a glance. In frequency distributions compiled from Table 3, a line drawn between 37 and 38 lateral-line scales (excluding intergrades) separates 86.8% of the western from 80.3% of the eastern, an average index of divergence (Ginsburg, 1954) of 83.6. Of 184 tabulated collections of *N. s. spilopterus*, specimens with 36 lateral-line scales were counted in only 17 (9.2%). Four more, each containing a single specimen, had counts of 37 only. All 163 others (88.6%) lacked specimens having a 36 count and had a large proportion of specimens with 38 or more. Most of the 36 counts were from the Ohio Valley, where gene exchange is most likely to occur between subspecies. In 65 collections of *N. s. hypsisomatus*, only 6 (9.2%) lacked a specimen with 36 scales, and of these, 5 contained only specimens with 37 scales, while the last was a single fish with 38. In only 29 collections, less than half the total (44.6%), were any specimens with 38 or more scales counted, whereas 38 is the mode in *N. s. spilopterus*.

In non-breeding specimens in certain areas, the lateral-line scale count is the only reliable basis for identifying a collection of *spilopterus* to subspecies, other than by purely geographical means. Certain collections from the Gasconade system in Missouri, and to a lesser extent some from the uppermost Mississippi and its tributaries, show a tendency toward a rather slender body form. In most collections of *N. s. hypsisomatus*, some specimens will approach *N. s. spilopterus* in form, and conversely, breeding specimens of the latter often become quite deep.

*Notropis whipplei*, *camurus*, and *lutrensis* are the only species of *Cyprinella* found in the range of *N. s. hypsisomatus*. All these forms have nine anal rays (*lutrensis* may show great variability), while *N. s. hypsisomatus* has eight.

From *lutrensis*, it differs in having usually 35 or more lateral-line scales, instead of 36 or less; in having a pharyngeal tooth present in the minor row which *lutrensis* lacks; and in lacking red pigment in the fins of breeding males. The body depth of *lutrensis* is probably greater, but measurements have not been made to corroborate this.





FIG. 4. Top: *Notropis s. spilopterus*, male, 58.8 mm. Monongahela drainage, Preston Co., W. Va.; upper middle: *N. s. hypsisomatus*, holotype male, 68.8 mm. Illinois drainage, McHenry Co., Ill.; lower middle: *N. s. hypsisomatus*, paratype male, 64.4 mm. Illinois drainage, McHenry Co., Ill.; bottom: nuptial tubercles on top of head and notal ridge of *Notropis spilopterus*.

From *camurus*, it differs in lacking a depigmented area at the base of the caudal rays; in having modally 14, sometimes 15 pectoral rays, instead of 15 or 16 (in about equal numbers in *camurus*); in having a smaller postdorsal length, usually 50% of standard length or less, instead of 51% or more; and in the sharper snout, which is notably blunt and rounded in *camurus*. Breeding males may be distinguished from those of *camurus* by the absence of an elongated dorsal fin, absence of red fin pigment, and by the presence of a hiatus between the tubercles of snout and top of head and a single row of tubercles on the mandibular rami (double in *camurus*).

From *whipplei*, it differs in having fewer lateral-line scales (usually 37 or 38 in *whipplei*) and less pectoral rays (modally 14 instead of 15), but these distinctions are not absolute. The best character to correlate with the different number of anal rays is the development of pigmentation in the dorsal fin. The relationship which is shown between *N. s. spilopterus* and *whipplei* in Tables 1 and 2 and Fig. 1 also holds for the new subspecies. Few specimens other than breeding males show more than a trace of pigment in the third interradiation membrane.

*Range* (Fig. 3.).—Illinois and Spring (trib. to Neosho) Rivers of the Arkansas system in Oklahoma, Arkansas and Kansas, and tributaries to the Mississippi River north of the Ohio River junction. In the Missouri system, it is found commonly only in the Gasconade. Specimens in Iowa lakes which drain into the Little Sioux River (Missouri system) are presumed to be the result of introductions. The report by Hankinson (1929) of "*Notropis whipplei*" in the Sheyenne River, Lisbon, N. D., a tributary to the Red River of the north, must be considered a doubtful possibility.

*Habitat*.—Little published information is available concerning the habitat of this subspecies. It apparently exists more commonly in warmer and more turbid waters than does the eastern subspecies. Judging from the occurrence of isolated populations in the Ozark systems (Gasconade, Meramec, Illinois, Spring), it, like the eastern subspecies, displays a propensity toward cooler, clearer waters. Starrett (1950a) records the subspecies over a number of different bottom types in the Des Moines River, Iowa.

*Etymology*.—*Hypsisomatus* is an adjective derived from the Greek *hypsi*, high or deep, and *soma*, body, in reference to the characteristic depth of the body.

#### NOTROPIS SPILOPTERUS : SPILOPTERUS x HYPISISOMATUS Intergrades

*Notropis whippelii spilopterus*—Greene, 1935: 108 (in part; Wisc. distr.).

*Discussion*.—The populations of *spilopterus* in Lake Michigan drainages are treated as intergrades principally because of their intermediacy in lateral-line scale number, which is the chief differentiating character for the two subspecies. Too few measurements have been made to allow corroboration. Since the area represents a meeting place between the two ranges, which, however, are not directly in contact at present, the presence of intergrades is quite plausible.

*Number of collections examined*.—Lake Michigan drainage, Michigan, 16; Lake Michigan drainage, Wisconsin, 10.

*Range*.—Eastern and western drainages into Lake Michigan.

## INTRASUBSPECIFIC VARIATION

*Notropis spilopterus* is a quite mobile, and apparently adaptable, species. For this reason, where there is fresh-water connection between river systems, differentiation tends to be weak or non-existent. On the other hand, while the species is capable of transgressing moderately effective barriers, it tends to be restricted to upland waters and to avoid the mainstream. It is no surprise, then, to find that the frequency distributions of certain characters of *spilopterus* show different degrees of skewness or different modal values from system to system. A perusal of Tables 3-6 and Fig. 2. will illustrate these differences.

TABLE 3.—Frequency distribution of lateral-line scales in *Notropis spilopterus*.

River System	34	35	36	37	38	39	40	41	N	$\bar{x}$	s	$\sigma\bar{x}$
Mohawk-Hudson...	—	—	—	3	20	15	1	1	40	38.4	.78	.13
Raritan.....	—	—	—	1	5	6	2	2	16	38.9	1.12	.28
Delaware.....	—	—	—	4	9	4	3	—	20	38.3	.98	.22
Susquehanna.....	—	—	1	18	78	48	3	1	149	38.3	.74	.06
Potomac*.....	—	—	1	35	52	14	1	—	104	37.7	.91	.09
St. Lawrence.....	—	—	—	1	10	4	—	—	15	38.2	.56	.14
Lake Ontario.....	—	—	—	1	22	23	6	1	53	38.7	.77	.11
Cayuga Lake.....	—	—	—	3	25	32	12	1	73	38.8	.83	.10
Lake Erie.....	—	—	1	8	32	23	—	—	64	38.2	.72	.09
Lake Huron.....	—	—	1	10	12	9	4	—	35	38.1	1.01	.17
Ohio (small tribs)...	—	—	3	18	36	21	7	—	85	38.1	.96	.10
Allegheny.....	—	—	1	2	14	13	3	—	33	38.5	.86	.15
Monongahela.....	—	—	—	2	26	22	2	—	52	38.5	.64	.09
Muskingum.....	—	—	—	1	4	3	—	2	10	38.8	1.32	.42
Kanawha.....	—	—	3	12	34	4	1	—	54	37.8	.74	.10
Guyandotte.....	—	—	—	—	2	5	—	—	7	38.7	.49	.18
Big Sandy.....	—	—	—	2	7	5	—	—	14	38.2	.70	.19
Scioto.....	—	—	—	3	10	2	—	—	15	37.9	.59	.18
Licking.....	—	—	—	8	10	2	—	—	20	37.7	.66	.15
Miami.....	—	—	1	10	19	8	3	—	41	38.1	.92	.14
Kentucky.....	—	—	—	9	9	3	—	—	21	37.7	.72	.16
Green.....	—	—	2	8	14	8	2	—	34	38.0	.98	.17
Wabash.....	—	—	1	21	28	6	—	—	56	37.7	.69	.09
Cumberland.....	—	—	4	9	20	12	1	1	47	38.0	1.04	.15
Tennessee.....	—	—	1	17	55	23	4	1	101	38.7	.82	.08
E. Lake Michigan..	—	—	2	3	6	—	—	—	11	37.4	.89	.27
W. Lake Michigan..	—	—	3	7	3	—	1	—	14	37.2	1.05	.28
Miss. R. (Wisc. N)..	—	1	11	11	2	—	1	—	26	36.7	.97	.19
St. Croix.....	—	—	3	5	4	—	—	—	12	37.1	.79	.23
Minnesota.....	—	3	4	2	—	—	—	—	9	35.9	.78	.26
Chippewa.....	—	2	2	4	6	4	—	—	18	37.4	1.29	.30
Black.....	—	—	3	3	—	—	—	—	6	36.5	.55	.22
Wisconsin.....	—	1	13	17	3	—	—	—	34	36.7	.69	.12
Rock.....	—	2	13	18	2	1	—	—	36	36.6	.80	.13
Illinois.....	1	1	39	73	19	3	—	—	136	36.9	.77	.07
Wapsinicon.....	—	2	10	7	—	1	—	—	20	36.6	.89	.20
Iowa.....	—	—	6	8	3	—	—	—	17	36.8	.73	.18
Des Moines.....	—	1	12	6	1	—	—	—	20	36.4	.67	.15
Miss. R. (S. Ill.)...	—	1	—	1	—	—	—	—	2	36.0	—	—
Meramec.....	—	—	5	4	1	—	—	—	10	36.6	.70	.22
Gasconade.....	—	1	8	31	7	—	—	—	47	36.9	.64	.09
Arkansas.....	3	20	29	2	1	—	—	—	55	35.6	.74	.10

\*One 32 not listed, but included in computations.

To what extent they are genetic or phenotypic is not certain, and the possibility of sampling error cannot be ignored. The distribution of lateral-line scale counts (Table 3, Fig. 2.) will serve as an example.

In the tributaries of the Ohio River, which contain the descendents of the ancestral stock of the Great Lakes and Atlantic Coast populations, there is comparatively little deviation from a mean of 38. The Allegheny and Monongahela show almost equal numbers of 38 and 39. The only others that fall any distance from the mean of 38, the Guyandot and the Muskingum, are based on small samples. Among these samples from the Ohio Valley are many with a mean of slightly less than 38. Of the five Atlantic Coast systems, two deviate greatly from a mean of 38. Of these, the Raritan, with a high mean, is based on a

TABLE 4.—Frequency distribution of pectoral rays in *Notropis spilopterus*.

River System	10	11	12	13	14	15	16	17	N	$\bar{x}$	s	$\bar{x}$
Mohawk-Hudson...	—	—	—	18	45	25	2	—	90	14.1	.75	.08
Raritan.....	—	—	—	2	13	23	5	—	43	14.7	.73	.11
Delaware.....	—	—	3	9	19	8	—	—	39	13.8	.85	.14
Susquehanna.....	—	—	2	70	168	40	5	—	285	13.9	.69	.04
Potomac.....	—	—	6	74	98	40	2	—	220	13.8	.79	.05
St. Lawrence.....	—	—	—	6	21	3	—	—	30	13.9	.55	.10
Lake Ontario.....	—	—	1	16	67	21	—	—	105	14.0	.63	.06
Cayuga Lake.....	—	—	1	37	81	26	3	—	148	14.0	.73	.06
Lake Erie.....	—	—	2	21	104	15	—	—	142	14.0	.42	.04
Lake Huron.....	—	—	1	17	47	5	—	—	70	13.8	.58	.07
Ohio (small tribs.)..	—	—	2	18	70	68	11	—	169	14.4	.81	.06
Allegheny.....	—	—	—	9	48	8	—	—	65	14.0	.52	.06
Monongahela.....	—	—	—	26	61	19	—	—	106	13.9	.65	.06
Muskingum.....	—	—	—	3	14	2	—	—	19	14.0	.52	.12
Kanawha.....	—	—	1	27	65	15	—	—	108	13.9	.64	.06
Guyandotte.....	—	—	—	1	9	6	2	—	16	14.7	.60	.15
Big Sandy.....	—	—	—	2	19	11	—	—	32	14.3	.58	.10
Scioto.....	—	—	—	6	16	7	1	—	30	14.1	.76	.10
Licking.....	—	—	—	3	11	25	3	—	42	14.7	.72	.11
Miami.....	—	—	1	15	39	27	—	—	82	14.1	.74	.08
Kentucky.....	—	—	—	7	15	20	—	—	42	14.3	.75	.12
Green.....	—	—	—	13	45	14	1	—	73	14.0	.65	.08
Wabash.....	—	—	1	16	57	37	1	—	112	14.2	.72	.07
Cumberland.....	—	—	—	13	53	49	5	—	120	14.4	.74	.07
Tennessee.....	—	—	1	36	129	53	5	—	224	14.1	.70	.05
E. Lake Michigan..	—	—	—	3	10	8	1	—	22	14.3	.78	.17
W. Lake Michigan..	—	—	—	2	18	5	3	—	28	14.3	.77	.15
Miss. R. (Wisc. N)..	—	—	—	6	28	15	3	—	52	14.3	.75	.10
St. Croix.....	—	—	1	9	9	5	—	—	24	13.8	.85	.17
Minnesota.....	—	—	—	6	7	4	—	—	17	13.9	.78	.19
Chippewa.....	—	—	—	2	23	6	5	—	36	14.4	.83	.14
Black.....	—	—	—	5	5	0	2	—	12	14.1	1.08	.31
Wisconsin.....	—	1	4	10	42	10	1	—	68	13.9	.85	.10
Rock.....	—	—	1	16	39	13	3	—	72	14.0	.80	.09
Illinois.....	1	1	4	56	153	51	6	1	273	14.0	.82	.05
Wapsinicon.....	—	—	—	13	26	1	—	—	40	13.7	.42	.07
Iowa.....	—	—	—	14	13	7	—	—	34	13.8	.77	.13
Des Moines.....	—	—	2	13	17	7	—	—	39	13.7	.82	.13
Miss. R. (S. Ill.)..	—	—	—	2	2	—	—	—	4	13.5	—	—
Meramec.....	—	—	—	1	9	7	3	—	20	14.6	.82	.18
Gasconade.....	—	—	—	13	48	31	4	—	96	14.3	.75	.08
Arkansas.....	—	—	—	26	46	37	1	—	110	14.1	.73	.07



fairly small sample, so that the difference may be due to sampling error. The more-adequately sampled Potomac population, however, cannot be explained easily by the same means. It will be noted in the next section that this population probably arose through a capture of part of the Ohio system, the Youghiogeny. Perhaps this slight shift to the low side in the Potomac is due, at least in part, to a retention of the genetic tendencies of the mother system, in which several systems show means of less than 38, whereas none of the other Great Lakes or Atlantic systems do. It is interesting that the populations in the Lake Ontario drainages and that in Cayuga Lake, which is essentially isolated,

TABLE 5.—Frequency distributions of two meristic characters in *Notropis spilopterus*.

River System	Pred. Circumf. Scales above LL								Anal rays			
	11	12	13	14	15	16	17	N	7	8	9	N
Mohawk-Hudson....	—	2	12	5	20	—	—	41	—	43	2	45
Raritan.....	—	—	10	2	8	—	—	20	—	21	1	22
Delaware.....	—	1	11	2	5	—	—	19	—	19	1	20
Susquehanna.....	1	3	92	23	31	—	—	130	—	138	14	152
Potomac.....	1	1	66	10	27	—	—	105	1	106	3	110
St. Lawrence.....	—	—	12	2	1	—	—	15	—	14	1	15
Lake Ontario.....	1	—	34	5	13	—	—	53	—	51	4	55
Cayuga Lake.....	—	—	53	4	16	—	—	73	—	70	4	74
Lake Erie.....	—	—	37	10	17	—	—	64	1	64	6	71
Lake Huron.....	—	—	23	5	6	—	—	34	—	35	—	35
Ohio (small tribs.)..	—	—	44	10	31	—	—	85	—	81	4	85
Allegheny.....	—	—	12	7	13	—	1	33	—	30	3	33
Monongahela.....	—	2	36	2	11	—	—	51	1	41	11	53
Muskingum.....	—	—	4	3	3	—	—	10	—	10	—	10
Kanawha.....	—	—	42	4	9	—	—	55	—	53	2	55
Guyandotte.....	—	—	2	2	3	—	—	7	—	8	1	9
Big Sandy.....	—	—	13	—	1	—	—	14	—	15	1	16
Scioto.....	—	—	10	1	2	2	—	15	—	12	3	15
Licking.....	—	—	10	3	7	—	—	20	—	18	3	21
Miami.....	—	—	27	4	9	—	—	40	3	35	3	41
Kentucky.....	—	—	11	5	5	—	—	21	—	20	1	21
Green.....	—	—	27	1	7	—	—	35	—	37	—	37
Wabash.....	—	1	41	4	10	—	—	56	1	51	4	56
Cumberland.....	1	3	40	3	8	—	—	55	—	56	4	60
Tennessee.....	—	4	88	5	10	—	—	107	1	103	8	112
E. Lake Michigan...	—	—	2	1	8	—	—	11	—	11	—	11
W. Lake Michigan...	—	—	12	2	—	—	—	14	—	13	1	14
Miss. R. (Wisc. N)...	1	1	21	1	2	—	—	26	—	26	—	26
St. Croix.....	—	1	11	—	—	—	—	12	—	12	—	12
Minnesota.....	—	1	8	—	—	—	—	9	—	9	—	9
Chippewa.....	—	—	13	—	4	—	—	17	—	16	1	17
Black.....	—	—	6	—	—	—	—	6	1	3	2	6
Wisconsin.....	1	—	27	6	—	—	—	34	—	30	4	34
Rock.....	—	2	31	1	2	—	—	36	—	30	6	36
Illinois.....	—	4	113	14	4	—	—	135	2	118	17	137
Wapsinicon.....	—	—	16	—	4	—	—	20	—	20	—	20
Iowa.....	—	—	15	—	2	—	—	17	—	17	—	17
Des Moines.....	—	—	16	2	2	—	—	20	—	20	—	20
Miss. R. (S. Ill.)...	—	—	2	—	—	—	—	2	—	2	—	2
Meramec.....	—	—	8	2	—	—	—	10	—	9	1	10
Gasconade.....	—	—	36	4	8	—	—	48	—	47	1	48
Arkansas.....	—	—	22	4	28	1	—	55	—	50	5	55

TABLE 6.—Frequency distributions of some proportional characters in *Notropis spilopterus*.

Dorsal Origin—Lateral Line																	Caudal Peduncle Depth									
Area	13	14	15	16	17	18	19	N	$\bar{x}$	s	$s\bar{x}$											$s\bar{x}$	s	$s\bar{x}$	s	$s\bar{x}$
Atlantic Slope....	2	3	8	6	4	—	—	23	15.3	1.18	.25											12	10	1	23	11.5
Great Lakes.....	—	2	17	9	5	—	—	33	15.5	.83	.15											3	19	11	—	33
Ohio Valley.....	6	18	33	15	7	—	—	79	15.0	1.04	.12											1	33	42	3	—
<i>S. spilopterus</i> .....	8	23	58	30	16	—	—	135	15.2	1.04	.09											1	36	73	24	1
Intergrades.....	—	2	1	—	—	2	—	5	15.8	—	—											4	1	—	5	11.2
<i>S. hypsomalus</i> ....	—	3	14	17	10	8	4	56	16.3	1.34	.18											—	4	28	19	5
																						—	—	—	56	11.5
																						—	—	—	76	10
Predorsal Length																	Orbit Length									
Area	50	51	52	53	54	55	56	N	$\bar{x}$	s	$s\bar{x}$											6	7	8	N	$\bar{x}$
Atlantic Slope....	—	—	1	8	9	5	—	23	53.8	.85	.18											—	20	3	23	7.1
Great Lakes.....	—	4	4	9	10	5	—	32	53.3	1.23	.22											—	20	13	33	7.4
Ohio Valley.....	—	4	12	18	35	8	2	79	53.2	1.38	.16											2	56	21	79	7.2
<i>S. spilopterus</i> .....	—	8	17	35	54	17	2	133	53.5	1.11	.10											2	96	37	135	7.3
Intergrades.....	—	—	2	1	1	1	—	5	53.2	—	—											—	3	1	4	7.3
<i>S. hypsomalus</i> ....	2	8	16	21	7	1	1	56	52.5	1.16	.16											2	40	13	55	7.2
																						—	—	—	49	.07
Postdorsal Length																	Head Length									
Area	46	47	48	49	50	51	52	N	$\bar{x}$	s	$s\bar{x}$											23	24	25	26	27
Atlantic Slope....	—	1	6	12	1	3	—	23	49.0	1.02	.21											—	5	8	8	2
Great Lakes.....	—	2	6	14	10	1	—	33	49.1	.93	.16											—	9	14	9	1
Ohio Valley.....	2	14	26	24	8	5	—	79	48.5	1.16	.13											3	18	29	25	4
<i>S. spilopterus</i> .....	2	17	38	50	19	9	—	135	48.7	1.12	.10											3	32	51	42	7
Intergrades.....	—	—	2	1	2	—	—	5	49.0	—	—											—	1	2	2	—
<i>S. hypsomalus</i> ....	1	—	9	9	23	10	4	56	49.8	1.19	.16											—	3	11	23	14
																						—	—	—	5	25.2
																						—	—	—	56	26.1
																						—	—	—	1.01	.14
Body Depth																	Upper Jaw Length									
Area	19	20	21	22	23	24	25	26	27	28	29	30	31	N	$\bar{x}$	s	$s\bar{x}$	7	8	9	N	$\bar{x}$	s	$s\bar{x}$	s	$s\bar{x}$
Atlantic Slope....	—	—	—	3	4	5	7	2	—	2	—	—	—	23	24.6	1.64	.34	3	20	—	23	7.9	.35	.07	.35	.07
Great Lakes.....	—	—	1	3	3	11	10	3	2	—	—	—	—	33	24.3	1.38	.24	7	26	—	33	7.4	.50	.09	.50	.09
Ohio Valley.....	1	1	8	13	21	19	11	3	1	1	—	—	—	79	23.3	1.58	.18	22	52	5	79	7.8	.55	.06	.55	.06
<i>S. spilopterus</i> .....	1	1	9	19	28	35	28	8	3	3	—	—	—	134	23.7	1.62	.14	32	99	5	136	7.8	.48	.04	.48	.04
Intergrades.....	—	—	—	2	1	—	—	1	—	1	—	—	—	5	25.2	—	—	—	1	3	—	4	7.8	—	—	—
<i>S. hypsomalus</i> ....	—	—	—	1	3	8	11	15	8	4	3	2	1	56	26.0	1.88	.25	16	36	3	55	7.8	.54	.07	.54	.07

both have a mode of barely 39, quite probably a result of common origin.

The intergrading populations in Lake Michigan have a mode of 37. The means are almost intermediate between the eastern and western subspecies. They fall lower than any population in the east, and higher than all but one in the west. This one is the Chippewa River, which sample is fairly small and has a wide distribution about the mean. Probably a larger sample would show a mean and distribution more typical of the western subspecies.

In the western subspecies, *N. s. hypsisomatus*, there are two populations, the St. Croix and the Chippewa, which have mean values of more than 37. The aberrant Chippewa has just been mentioned. The St. Croix has a mode of 37, but the small sample is almost equally divided into a range of three counts. With two further exceptions, the means of the populations of the western subspecies are between 36.0 and 36.9, and the modes are 36 or 37, often in almost equal numbers. The Minnesota River sample falls out, the small sample having a disproportionate number of 35 counts, but a mode of 36. In the two tributaries of the Arkansas, the Illinois and Spring Rivers, there is a strong tendency toward a lower scale count, there being a large number with 35 or less scales. There is a good possibility that this is due to introgressive hybridization with *Notropis lutrensis*, which usually occupies a somewhat different niche, but occurs in close proximity. These Arkansas system populations could be considered a third subspecies using a loose criterion, but this would be unwise. It is tempting to postulate that the general approach of *N. s. hypsisomatus* to *N. lutrensis* is due to introgression, but the evidence is lacking. It seems improbable, with their different ecological preferences, that the two species occupied the same range while differentiation was taking place.

Proportional measurements have been recorded according to major areas of distribution—the Atlantic slope, Great Lakes, Ohio Valley, intergrade area in Lake Michigan, and the West. The tendencies toward differentiation between the two subspecies in these characters are evident in the tables. In addition, there are some minor differences between the populations of the eastern subspecies which are interesting, but which are difficult to interpret except to attribute them to chance or to small adaptive changes. The Ohio Valley population is significantly different from those of the Atlantic slope and the Great Lakes in two characters which reflect body depth—body depth *per se* and caudal peduncle depth. In both these, it falls toward the lower limit, and well away from the deep-bodied *hypsisomatus*. This would appear to be further evidence for the lack of gene flow between the two subspecies in their present situation.

#### DISPERSAL AND SPECIATION

Two subspecies of *Notropis spilopterus* are recognized, one in the eastern United States and Canada, and one in the mid-western United States. The Atlantic Coast and Great Lakes populations of *N. s. spilopterus* are completely separated from the western subspecies at present. The avenue for contact between the populations inhabiting the Ohio (including the Tennessee) and those of the West does exist.

Few collections of the western *N. s. hypsisomatus* are available from lower Illinois, and none have been seen from south of the Meramec River on the Missouri side of the Mississippi. The most likely region for gene exchange between the subspecies is, therefore, apparently sparsely inhabited by them. Although *N. s. hypsisomatus* may be less so, the species, *spilopterus*, as a whole is an upland form, preferring moderate-sized streams, but not small headwaters, leaving the main-stream and larger waters to the related species, *whipplei*. Although this relationship is not absolute, the Mississippi River below the Ohio nevertheless appears to be a potent and effective barrier, and is probably the principal deterrent to genetic mixing of the two subspecies.

There is good probability that *Notropis spilopterus* was widely distributed in the preglacial Teays River (Janssen, 1953), in both the western extension, which is now a portion of the Missouri system, and the eastern, which drained essentially the present upper Mississippi and lower Ohio valleys. The Tennessee and Cumberland Rivers were probably, at some time at least, tributaries to this "master stream of a primeval America".

The process of subspecific differentiation may have been initiated as early as the Nebraskan or Kansan glacial stage, when, at maximum development, the ice sheet is represented as having reached northern Missouri and southern Illinois. The range of *spilopterus* would thus have been split into two major parts. In the east the species would have been forced into what is now the Ohio system and its southern tributaries.

The western population, cut off by glacial ice or by a large and torrentous Mississippi, must have been concentrated in one or both of two refugia—the Ozark region or the driftless area of Wisconsin. The two regions may not have been completely isolated from one another, even at maximum glaciation, for the driftless area was never completely surrounded by ice (Flint, 1947: 240). The Ozark region is the more likely center of origin for *N. s. hypsisomatus*, for the presence of isolated, presumably relict, populations in the Spring and Illinois Rivers (Arkansas River tributaries) and in the Gasconade and Meramec, militates against postglacial dispersion to these systems from the driftless area, and argues for a formerly wider distribution in the Ozarks and surrounding areas. Further, the apparent adaptation of this subspecies to warmer waters seems to indicate a more southerly origin.

Its presence in the two southwestern Ozark streams is probably due to headwater capture when its range was wider, for the nearest population at present is in the Gasconade. Between these populations, the White and Osage rivers intervene. This strongly suggests the former existence of this form in the Osage, and possibly in the White. If it had once existed in the White, however, there is no observable reason for its absence at the present time, for the habitat seems favorable, and the presence of the related *N. galacturus* would seem no particular drawback, in view of its coexistence with *N. s. spilopterus* in the Tennessee and Cumberland systems. Presumably *N. s. hypsisomatus* was never widespread in the Arkansas system, but has always been restricted to a few of its upland tributaries.



During interglacial stages, dispersal doubtless took place, only to have the range restricted again by glacial advances. Perhaps a stock, already differentiated in the Ozark refugium, invaded the driftless area before the Wisconsin glaciation and persisted there. If this were true, the present distribution of *N. s. hypsisomatus* would be the result of dispersal from two centers, one primary and one secondary.

Changing conditions since the end of the Wisconsin glaciation have caused the obliteration of *N. s. hypsisomatus* over much of its southern range. Except for the relicts in the Ozarks, the form has become extinct in the Arkansas and Missouri systems with the return of semi-arid conditions.

At the same time that the southwestern range was being contracted during the Wisconsin glacial retreat, glacial lake and stream connectives provided pathways which allowed extension of the range into favorable areas to the north and east. Neither subspecies appears to favor extremely cold waters, a factor which limits the present range and presumably rendered the species unable to take advantage of many glacial routes. At present *N. s. spilopterus* is an uncommon resident of the St. Lawrence River and the northern shore of Lake Ontario, and apparently does not extend entirely around the lower peninsula of Michigan. The northern limit seems to be quite sharp. Following the Wisconsin glacier as it retreated, *N. s. hypsisomatus* seems to have used the early St. Croix outlet and Fox connectives in Wisconsin, for it is found above St. Croix and Chippewa Falls, and intergrades are found in Lake Winnebago and tributaries to Green Bay. It did not, however, enter or survive in glacial Lake Duluth; otherwise it would be expected in Lake Superior.

*N. s. spilopterus* probably entered the Great Lakes drainage through the glacial Maumee (Ft. Wayne) outlet and followed the early lakes as they grew in extent to the east. (For diagrams of Great Lakes development see Radforth, 1944: 13-18; Flint, 1947: 258, or others.) At about the time of glacial Lake Warren, it entered the Finger Lakes region of New York, and later became established in the Mohawk-Hudson system while this drained Lake Lundy or, later, Lake Iroquois, after the closure of the westward-draining Grand outlet into Lake Chicago. Finally, since the withdrawal of the Champlain Sea, it has inhabited the St. Lawrence River.

The Susquehanna River population probably became established through contact, via the glacial Canisteo outlet (Fairchild, 1908), with the Genesee system, which had received its stock from the Ohio Valley as described above.

The Potomac River stock could have been derived from the Susquehanna at the time when Chesapeake Bay contained the extension of that system (Shattuck, 1906) and those rivers from the James to the Potomac were tributaries, but this is unlikely, for the species is not found in the other tributary systems, which were surely suitable habitat. It could have been the result of stream capture between the Potomac and the Susquehanna. The most acceptable assumption, however, seems to be that the Potomac population originated, independent of the Susquehanna, by means of stream capture of a portion of the Youghiogeny (Monongahela system) by the Potomac.

The presence of intergrades in Lake Michigan and its tributaries in Wisconsin and Michigan is suggestive of actual contact between *N. s. spilopterus* and *N. s. hypsisomatus* in that area at one time. The dispersal of Wisconsin forms has already been traced to the present Lake Winnebago and Green Bay. Although relatively recent stream capture would be the preferable hypothesis in dispersing *N. s. spilopterus* from Lake Huron to Lake Michigan, the prominent glacial Grand outlet cannot be ignored, and the transfer is tentatively attributed to it. Why the subspecies did not greatly contaminate the *N. s. hypsisomatus* which was presumably present in the Chicago outlet of Lake Michigan is unknown, but presumably some ecological barrier existed which prevented their complete mixing.

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## Studies on the Growth of the Leaf of *Guarea*

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The perennial leaf of *Guarea rhopalocarpa* Radlk, a species native to Costa Rica, has been described by Skutch (1946). He reported that the leaves of this tree persisted for many years and made annual increments of growth. This condition he believed to be unique among higher plants. As this tree grows in the mountains in heavy jungle, he was unable to make thorough growth studies. Sonntag (1887) stated that the true apical growth of the leaves of *Guarea* persisted for relatively short periods. Growth, according to him, was not from a true meristem but from pre-formed embryonic leaves. Despite the widespread botanical interest in this plant for so many years, no detailed study of its growth habit has appeared in the literature.

Our paper describes the growth and regeneration of the leaf of *Guarea trichilioides* L. Mant. (*Guarea Guara* (Jacq.) P. Wilson), a tree endemic to Puerto Rico. The species is widely distributed in Puerto Rico, where it is useful for timber, and is known locally as "guara guao."

### MATERIALS AND METHODS

Several 30-40 ft. trees of *G. trichilioides* were used as a source of experimental material. The main trunks branched at a height of 5-7 ft. and the branches could be reached easily from the ground or with a stepladder.

The growth habit, flowering and fruiting, etc., were studied over a period of about four years. Seedling plants also were grown. Leaf and stem cuttings were taken from mature trees and from seedlings for studies on root formation.

### DESCRIPTION OF THE LEAF

The leaves are pinnately compound with several pairs of leaflets, each mature leaflet being about 25 cm. long and 5 to 8 cm. broad. The end of the rachis is terminated by leaflets, which are folded upward, with involute margins. The tip of the rachis is covered with short hairs but there are no scales. The tips give rise to new lengths of rachis bearing additional pairs of leaflets. Three to four new pairs of leaflets are formed, and each leaf extends itself 10-15 cm. The largest leaf seen in Puerto Rico was 80 cm. long. A photograph of a leaf is shown in fig. 1.

The diameter of the rachis varied from 5 mm. near the base to 1.0 mm. in the elongating portion. There is a swelling at the base where the rachis merges with the branch. This swelling averaged 8 mm. in diameter. There is an active cambium in the rachis and secondary wood is produced. However, no annual rings were observed. Terminal

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growth in the leaves coincided with the flushes of growth in the tree, which occurred mainly in July and August. There was a second flush of stem and leaf growth in November. Each leaf, however, elongated only once a year. Leaves remained on the tree for two to three years.

*Elongation of the rachis.*—Various rachises were marked off in cm. or mm. with India ink to measure the rates and regions of elongation. Ten resting rachises were marked and 10 in active growth. Elongation occurred only from the tip. Once growth was initiated, regions of elongation extended over a space of 2–3 cm. Growth, therefore, resembled that of a stem.



FIG. 1. Actively growing leaf of *Guarea trichilioides*. Elongation occurs from the apex meristem and is completed in two to three weeks. The leaflets on one side of the rachis have been removed.

FIG. 2. Well-rooted leaves of *Guarea trichilioides*. These leaves were placed under a mist spray in the greenhouse for approximately six weeks.

*Regeneration of the leaf.*—Numerous attempts were made to induce leaves from mature trees to form roots. One hundred and thirty marcots (air-layers) were made by girdling the rachis and applying indoleacetic acid (IAA), indolebutyric acid (IBA) or naphthalenacetic acid (NAA), at concentrations of 0.1 to 0.2 per cent in lanolin to the cut surface. These were then covered with moist sphagnum and wrapped with polyethylene plastic. Both treated and untreated rachises formed a large callus around the girdle, but failed to regenerate roots. Leaf cuttings from mature trees were smeared at the base with 0.02 per cent IAA, IBA, naphthoxyacetic, triiodobenzoic or 2,4-dichlorophenoxyacetic acid in lanolin and placed under a mist spray for 6 hrs. daily. Only 2 (controls) out of 200 formed roots, and these failed to survive when transplanted.

It is well known that cuttings from young plants are frequently better able to form roots than are cuttings from old trees. Leaves from 2-year-old trees of *Guarea trichilioides* were planted under a mist spray in sand or vermiculite. Rooting was more rapid in the vermiculite, but 84 per cent of all cuttings formed good root systems within 8 weeks without special treatment. Examples of rooted leaves are shown in fig. 2.

*Flowering and fruiting.*—Flowers and half-grown fruits occur on the trees, simultaneously, in July and August, and in October and November. The white flowers were produced in racemes 12–14 cm. long, and the fruit is a capsule containing many red seeds. The blossoms and fruits are shown in fig. 3.



FIG. 3. Flowers and fruits of *Guarea trichilioides*. Flowers and mature fruits are found on the trees in July and in November.

#### GROWTH OF SEEDLINGS

Seeds germinated readily in sand beds. It was necessary to protect the young shoots against slugs, which otherwise kept them cut down to ground level. Ten plants were grown for observation. In 24 months, they averaged 1.1 cm. in diameter at 15 cm. above ground level and were 74.6 cm. tall. The first 8–10 leaves were simple, and no pinnate leaves were produced for the first 22 months. The first

2-3 pinnate leaves lacked a growing point. After this time, nearly all the leaves had a growing point and 3-5 pairs of leaflets when formed.

*Regeneration of branch cuttings.*—Branch cuttings of mature trees failed to root under a mist spray despite treatment with 0.2 per cent IAA, IBA, or NAA. Under the same conditions 38 per cent of the cuttings from the seedling trees formed roots readily in 8 weeks without treatment.

#### GROWTH OF ROOTED LEAVES

Well-rooted leaves established in soil in clay pots have been kept under observation for three months. In about half of the leaves the tip of the rachis died. Most of the remaining leaves are still dormant, although 4 have produced new and apparently normal growth consisting of 3-5 pairs of leaflets and 5 cm. of rachis.

#### DISCUSSION

The leaf of *Guarea trichilioides* makes increments of growth from the apex. These leaves persist for two to three years. Whether this growth is from a true meristem or from embryonic pre-formed leaves was not determined. No annual rings of growth were observed in the rachis although there is an active cambium. Leaves from 2-year-old trees formed roots more readily than those from mature trees. Branch cuttings behaved in the same way.

The leaves of many herbaceous plants may be rooted (Priestley and Swingle, 1929) but in these instances, the leaf either has no capacity for further growth or it regenerates a new stem bud, usually from callus tissue. Rooting of leaves from woody plants is less common but has been reported in lemons by Halma (1931) and in the cotyledons of *Hevea* (Muzik, 1957). A situation where the leaf produces new growth from the apex, as in *G. trichilioides*, appears to be unique.

#### SUMMARY

The leaf of *Guarea trichilioides* produced annually 10-15 cm. lengths of rachis for at least three years. This growth was produced from the apex, and resembles in habit that of a stem. Branch cuttings and leaves from young plants regenerated roots readily but branch cuttings and leaves from old plants did not.

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## Distribution of Rutin and Other Flavonoid Substances in Mature Buckwheat Plants<sup>1</sup>

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Rutin (3, 5, 7, 3', 4'-pentahydroxyflavone-3-rutinoside) has long been recognized as a constituent of buckwheat. Schunk (5) isolated it from leaves, Wunderlich (8) from flowers, and Brandl and Schärtel (2) from both sources. From the occurrence of unidentified impurities in buckwheat rutin preparations it has been concluded (3) that small amounts of other flavonoid compounds may also be present in the plant. This view has been supported by recent quantitative studies in which contents of rutin and total flavonol have been compared (1, 4). As part of an effort to characterize the flavonoid constituents of buckwheat more exactly so that the plant might be useful in studies of flavonol biogenesis, green and etiolated seedlings have been examined qualitatively (6) and semi-quantitatively (7). Four other flavonoids in addition to rutin were found in such material. In the present work this descriptive study of buckwheat is extended by examining mature plants and noting the occurrence therein of the same five flavonoids found in seedlings.

### METHODS

Plants of *Fagopyrum sagittatum* Gilib. (*F. esculentum* Moench) var. Japanese were cultured to maturity both in the field and in the greenhouse. From time to time plants of both groups were harvested, divided into their constituent organs, and extracted immediately with 95% ethanol at room temperature. Each extract was concentrated to a small volume *in vacuo* and used in this form. In order to relate the flavonoids of one sample with those of another and with those present in seedlings procedures of two-dimensional paper chromatography, color reactions in visible and ultraviolet light, and absorption spectrophotometry were used. The manner of employment of these techniques has already been described in detail (6).

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## RESULTS

Results of this study are presented in Table 1 and require little elaboration. Although no flavonoid substance could be detected in the roots, rutin was found in every other organ. In no case was uncombined quercetin, the aglycone of rutin, present in a detectable amount. The four unidentified flavonoids—A, B, C, and D—previously shown to occur in seedlings (6) were also present in mature plants. Substance C was found in stems and hypocotyls, and substance D in flowers. The whole fruits contained all five flavonoids; of these, Substances A, B, C, and D were localized exclusively in the pericarps.

TABLE 1.—Distribution of rutin and unknown flavonoid substances in organs of mature buckwheat plants. P—present.

Organ	Substance					
	A	B	C	D	Rutin	Chl
Leaf.....	—	—	—	—	P	P
Stem.....	—	—	P	—	P	P
Hypocotyl.....	—	—	P	—	P	P
Root.....	—	—	—	—	—	—
Flower.....	—	—	—	P	P	P
Fruit.....	P	P	P	P	P	P

Also present in all organs except roots was an unknown substance, here designated "Chl", which in color reactions, chromatographic behavior, and absorption spectra closely resembled chlorogenic acid. From comparison with an authentic sample, however, it could not be concluded that Substance Chl is identical with this common plant constituent.

The curious fact that while the most abundant flavonoid, rutin, occurs throughout most of the plant the other substances appear to be sharply localized in distribution remains to be explained. Nevertheless, the present data should enable a more rational selection of buckwheat material for experimental studies of flavonoid biosynthesis.

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